Anticipation in the retina and the primary visual cortex : towards an integrated retino-cortical model for motion processing

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Anticipation in the retina and the primary visual cortex : towards an integrated retino-cortical model for motion processing

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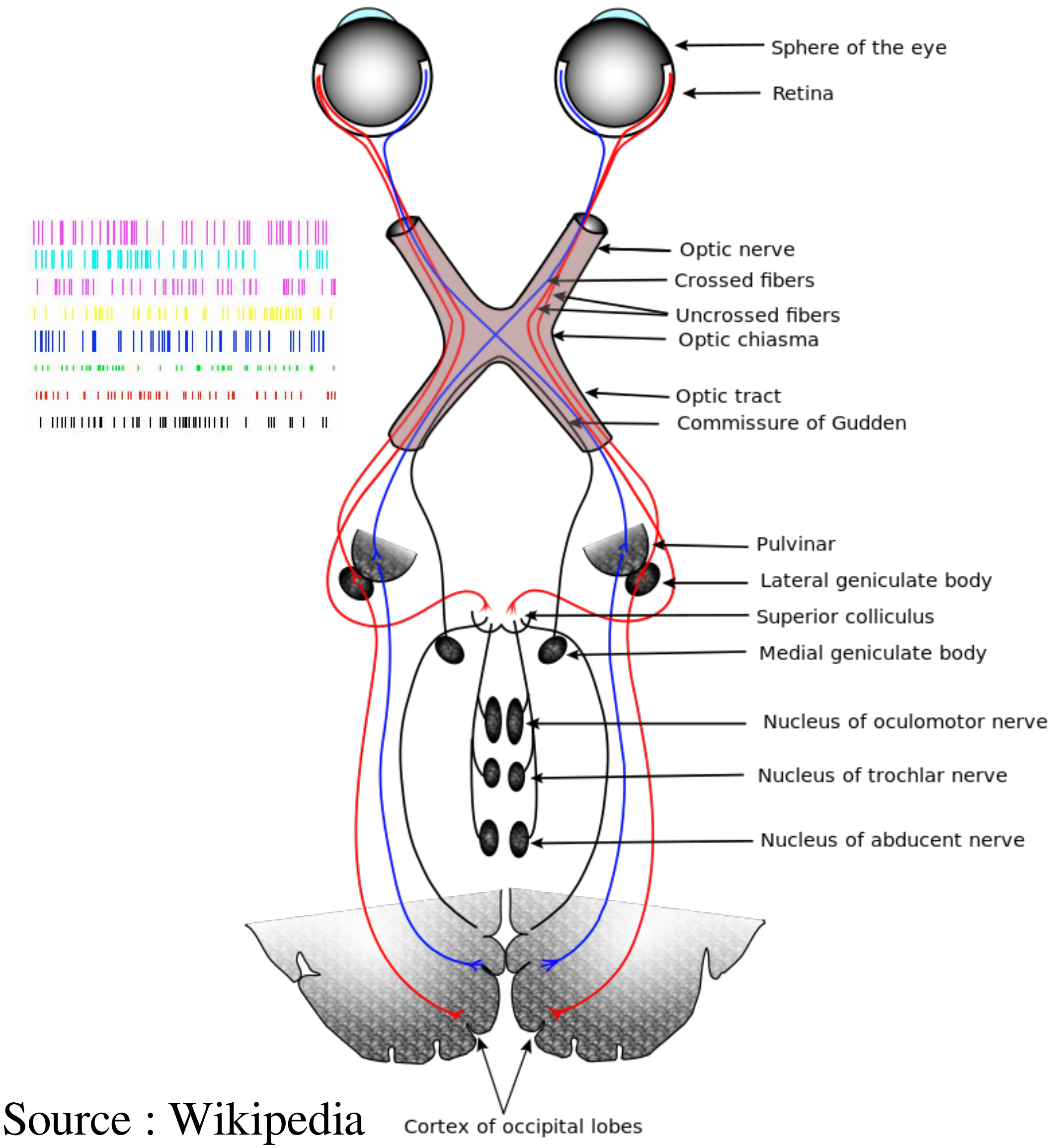
Alain Destexhe

Frédéric Chavane
Sandrine Chemla

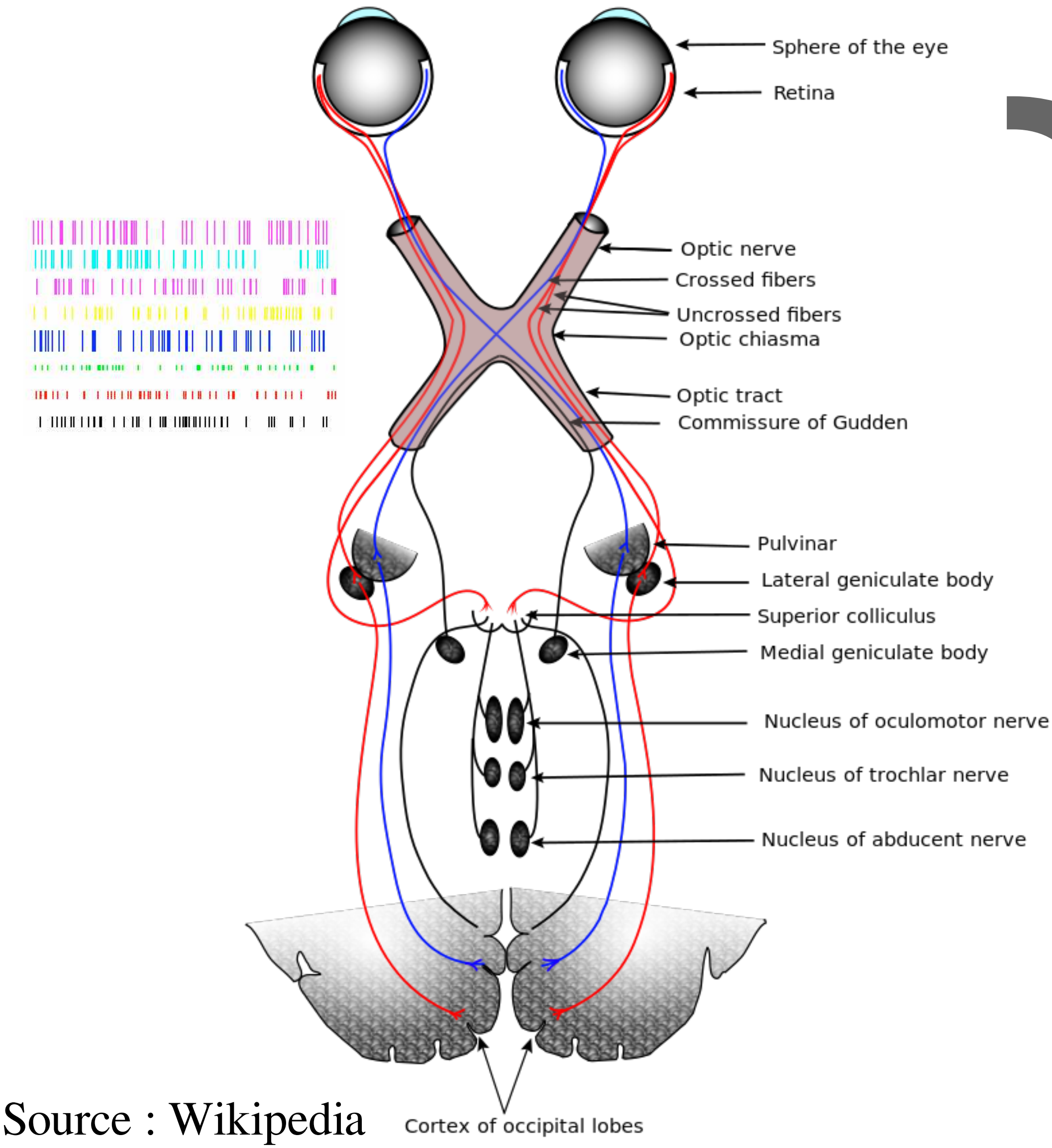
Olivier Marre

The visual flow



Source : Wikipedia

The visual flow



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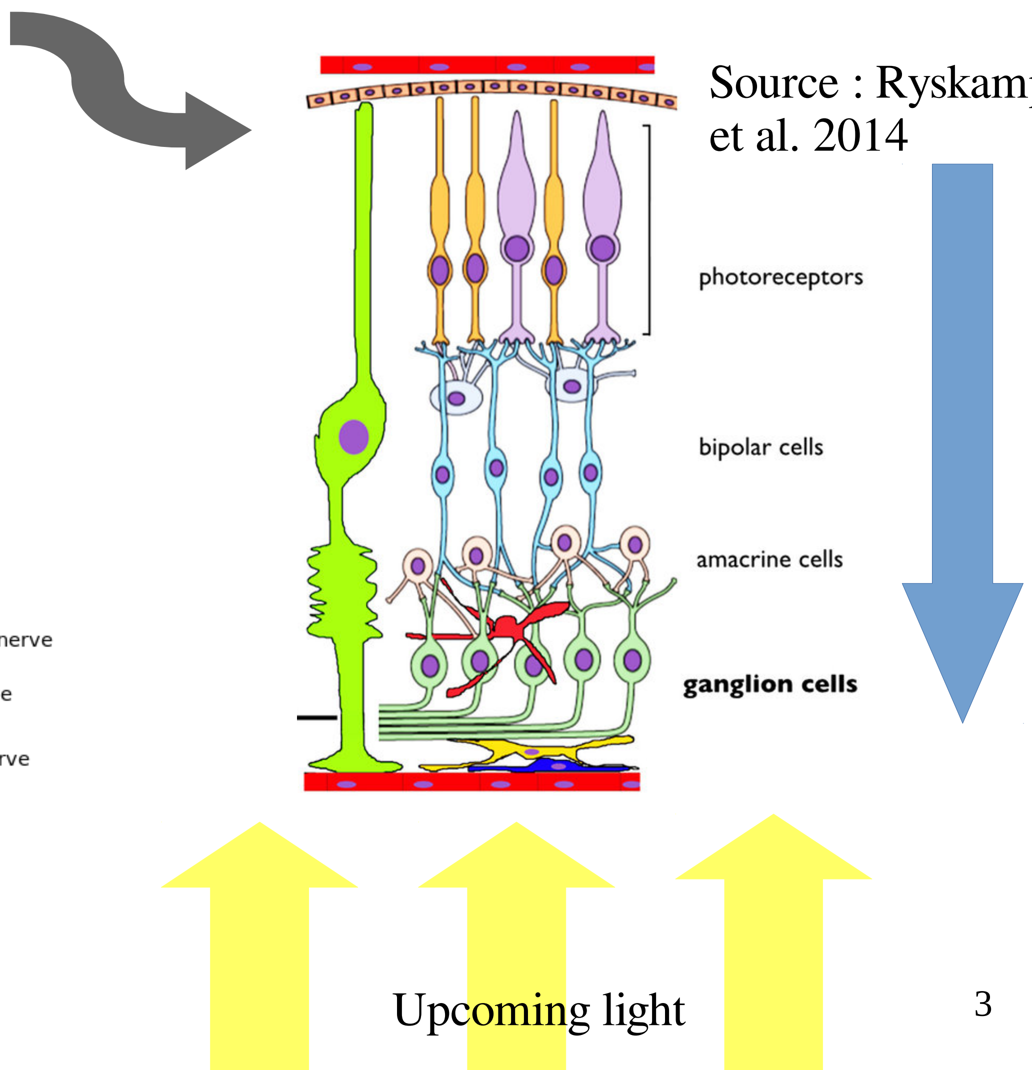
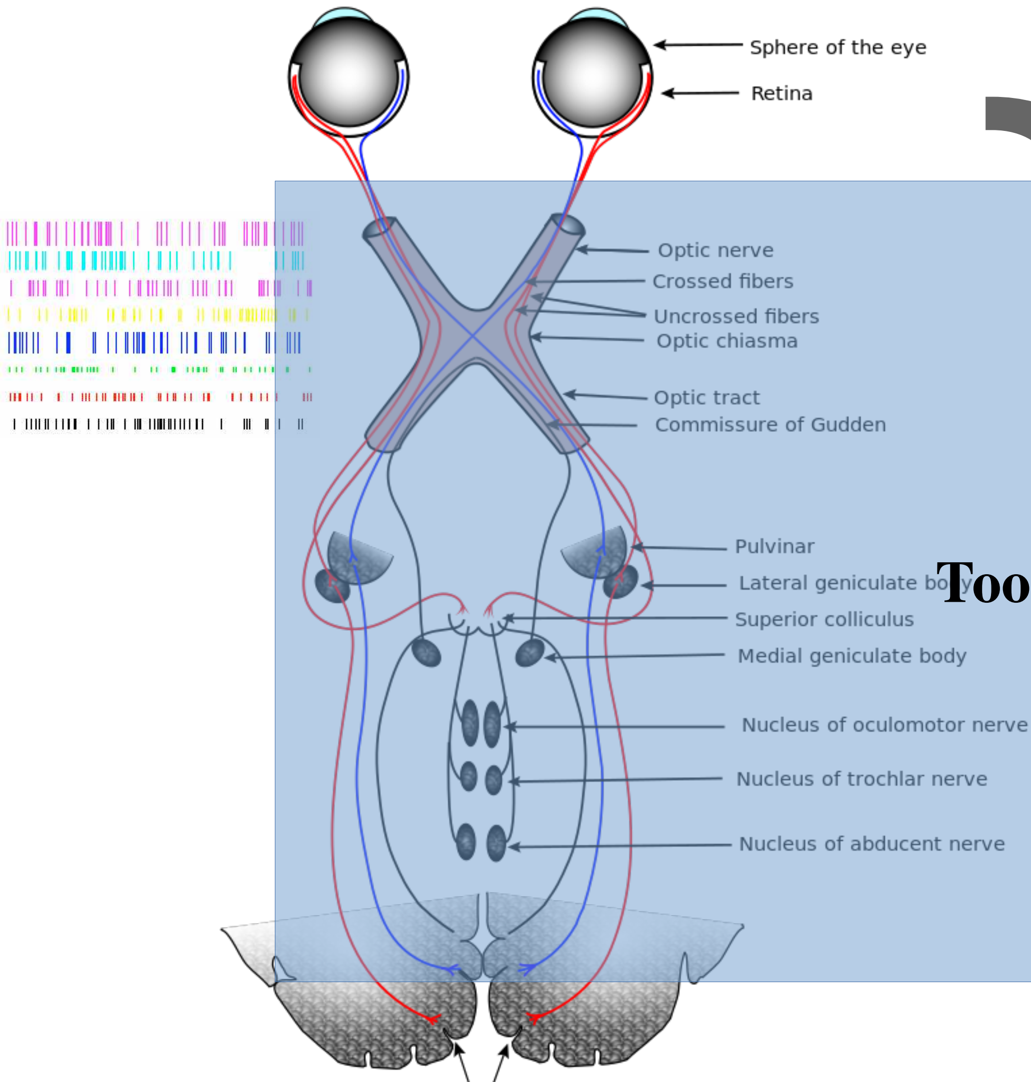
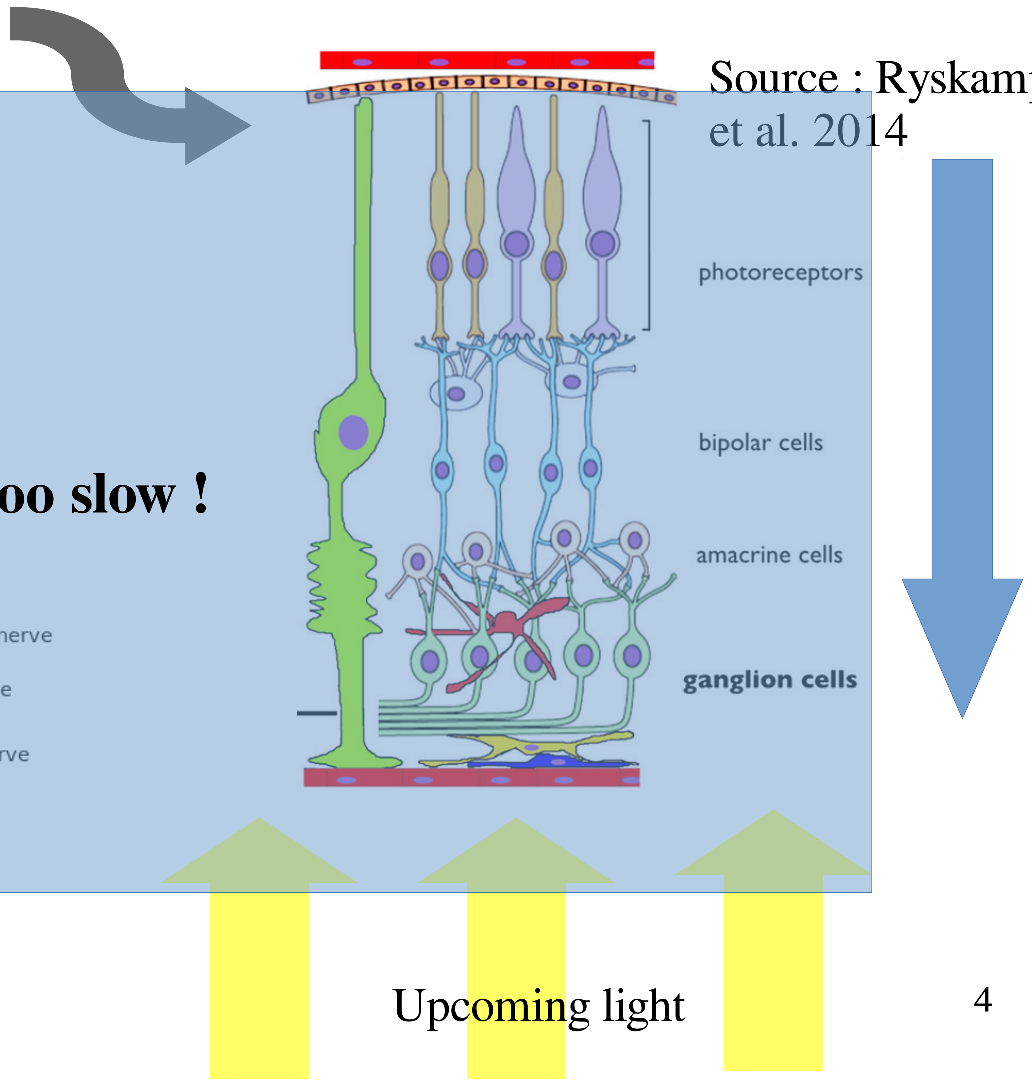


Source : Ryskamp et al. 2014

The visual flow



Too slow !



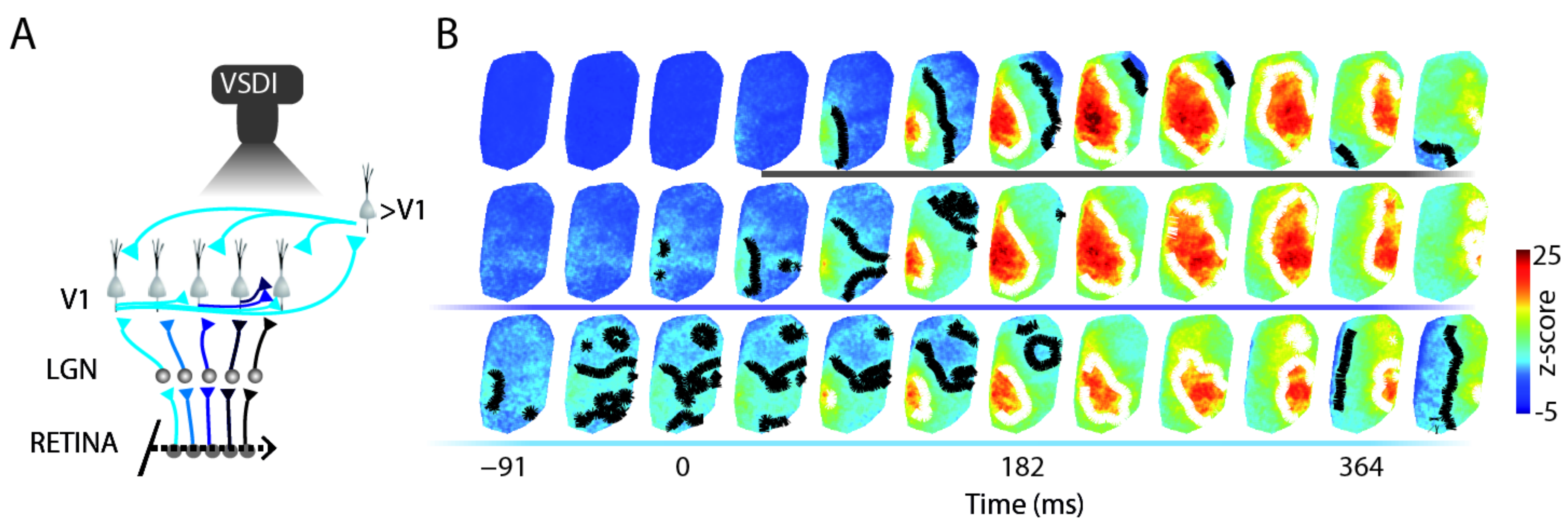
Source : Ryskamp et al. 2014

Upcoming light

Source : Wikipedia

Stating the problem : Visual Anticipation

Anticipation is carried out by the primary visual cortex (V1) through an activation wave

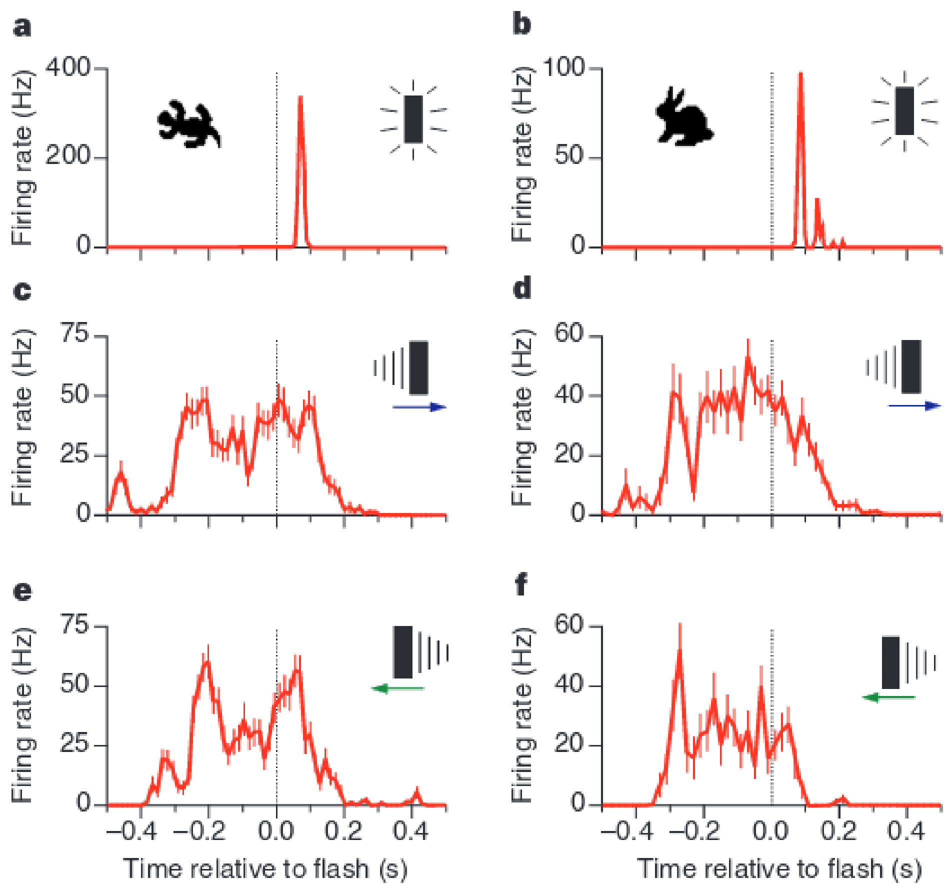


Source : Benvenutti et al. 2015

Stating the problem : Visual Anticipation

But the retina is not a mere transmitter, it is able to perform many computations such as :

- Orientation sensitivity
- Contrast gain control
- Sensitivity to differential motion
- .... and « **Motion Anticipation** »



Source : Berry et al. 1999

Stating the problem : Visual Anticipation

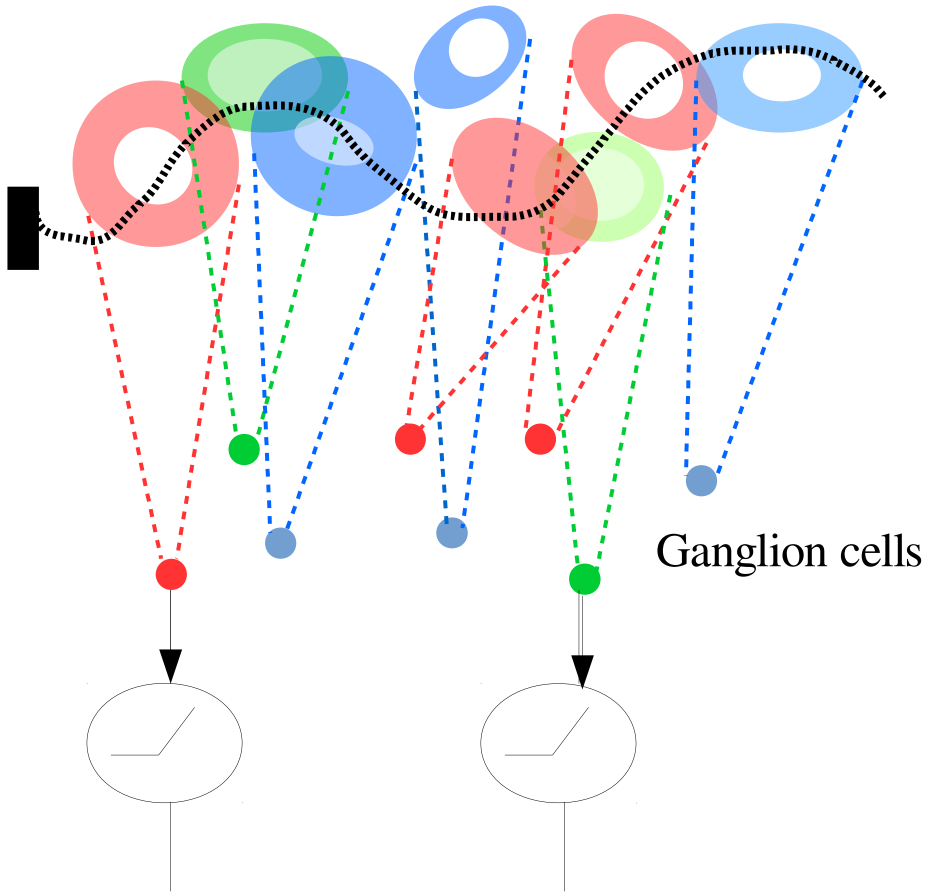
- **What are the respective :**
- **Mechanisms underlying retinal and cortical anticipation?**
- **Role of each part ?**

I) Anticipation in the retina

The Hubel-Wiesel view of vision

Nobel prize 1981

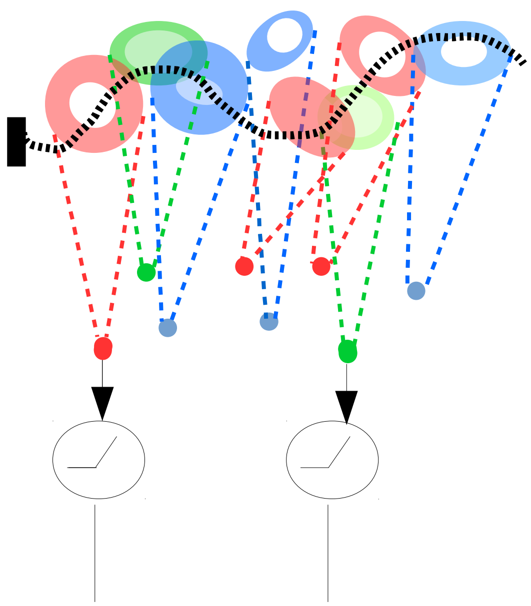
Ganglion cells response is the convolution of the stimulus with a spatio-temporal receptive field followed by a non linearity

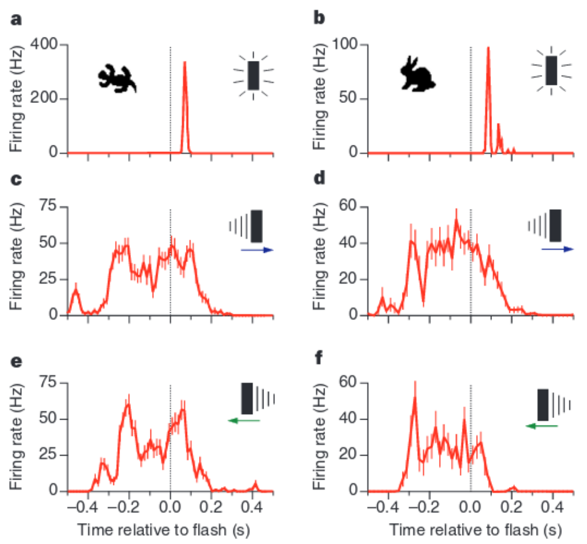


Ganglion cells are independent encoders

The Hubel-Wiesel view of vision

Nobel prize 1981



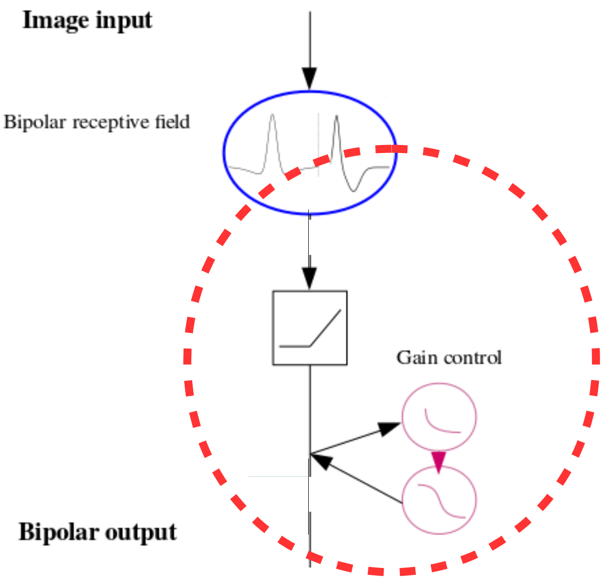


Source : Berry et al. 1999

- **Which mechanism can account for motion anticipation in the retina ?**

Building a 2D retina model for motion anticipation

1) Gain control (Chen et al. 2013)



- Bipolar voltage :

$$\left[K_i \overset{S,t}{*} \mathcal{S} \right](t) = \int_{-\infty}^{t} K_T(t-u) \left[\int_{\mathbb{R}^2} K_{i,S}(x,y)\, \mathcal{S}(x,y,u)\, dx\, dy \right] du$$

- Non-linear function :

$$\mathcal{N}_B(V_{B_i}) = \begin{cases} 0, & \text{if} \quad V_{B_i} \leq \theta_B; \\ V_{B_i} - \theta_B, & \text{else.} \end{cases}$$

- Activation function :

$$\frac{dA_{B_i}}{dt} = -\frac{A_{B_i}}{\tau_a} + h\mathcal{N}(V_{B_i}(t)).$$

- Gain Control function :

$$\mathcal{G}_B(A) = \begin{cases} 0, & \text{if} \ A \leq 0; \\ \frac{1}{1+A^6}, & \text{else.} \end{cases}$$

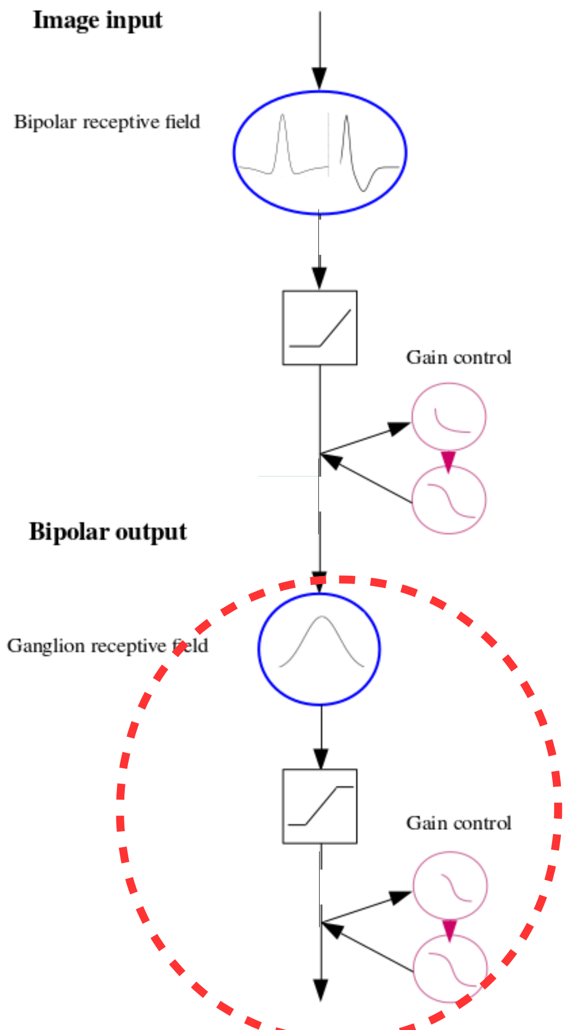
- Output :

$$R_{B_i} = \mathcal{N}_B\left(V_{B_i}\right) \mathcal{G}_B\left(A_{B_i}\right).$$

Building a 2D retina model for motion anticipation

1) Gain control (Chen et al. 2013)

Feedforward flow



- Ganglion voltage

$$V_{G_k} = \sum_i W_{G_k}^{B_i} R_{B_i}$$

- Non-linear function :

$$\mathcal{N}_{G_F}(V) = \begin{cases} 0, & \text{if} \quad V \leq 0; \\ \alpha_{G_F}(V - \theta_{G_F}), & \text{if} \quad \theta_{G_F} \leq V \leq N_{G_F}^{max}/\alpha_{G_F} + \theta_{G_F} \\ N_{G_F}^{max}, & \text{else}. \end{cases}$$

- Activation function :

$$\frac{dA_{G_{F k_F}}}{dt} = -\frac{A_{G_{F k_F}}}{\tau_{G_F}} + h_{G_F} \mathcal{N}_{G_F}\left(V_{G_{F k_F}}\right)$$

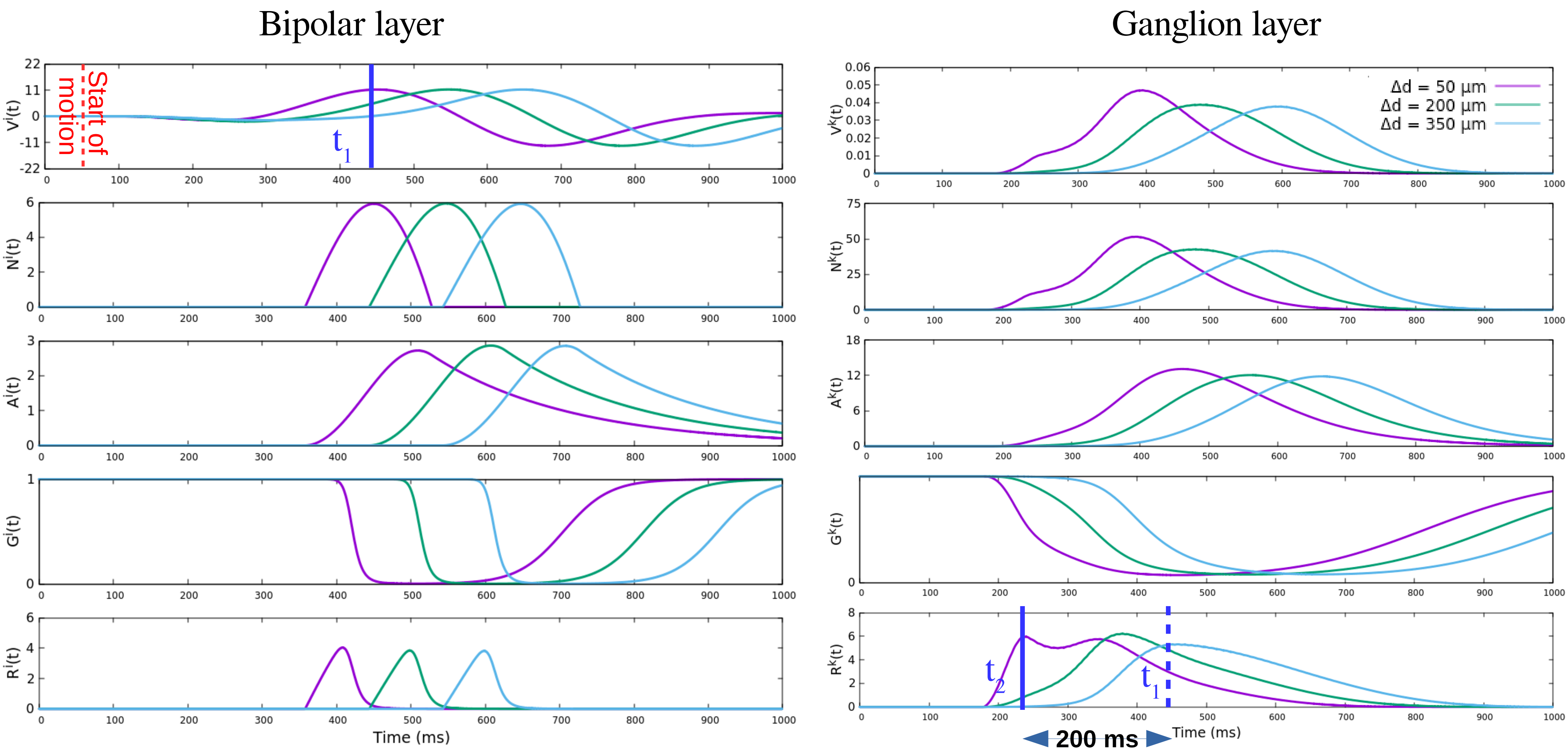
- Gain Control function :

$$\mathcal{G}_{G_F}(A) = \begin{cases} 0, & \text{if} \quad A \leq 0; \\ \frac{1}{1+A}, & \text{else}. \end{cases}$$

- Output :

$$R_{G_{F k_F}}\left(V_{G_{F k_F}}, A_{G_{F k_F}}\right) = \mathcal{N}_{G_F}(V_{G_{F k_F}})\,\mathcal{G}_{G_F}(A_{G_{F k_F}}).$$

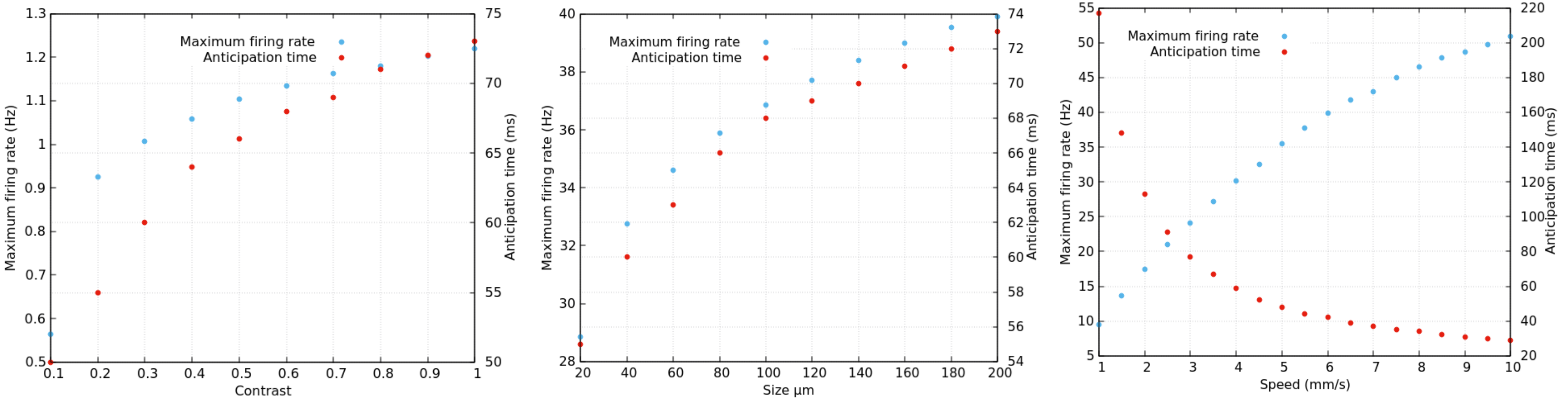
1D results : smooth motion anticipation with gain control



Anticipation time = $|t_1 - t_2|$

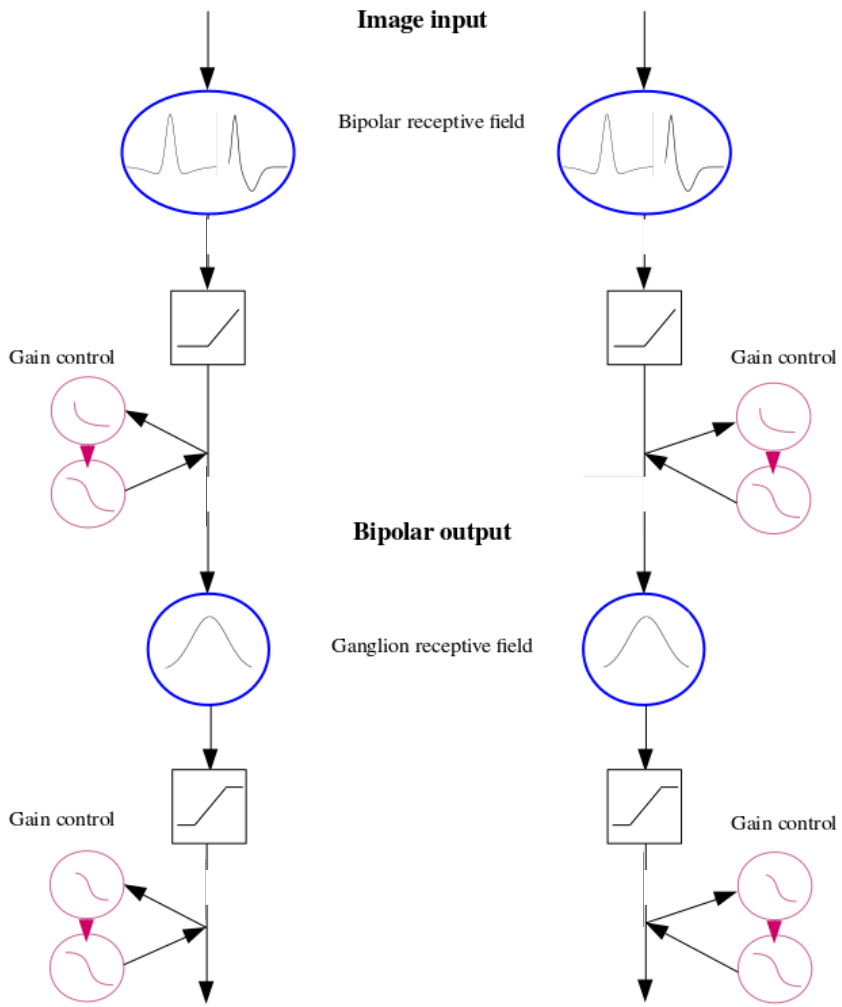
1D results : smooth motion anticipation with gain control

Anticipation variability with stimulus parameters



Building a 2D retina model for motion anticipation

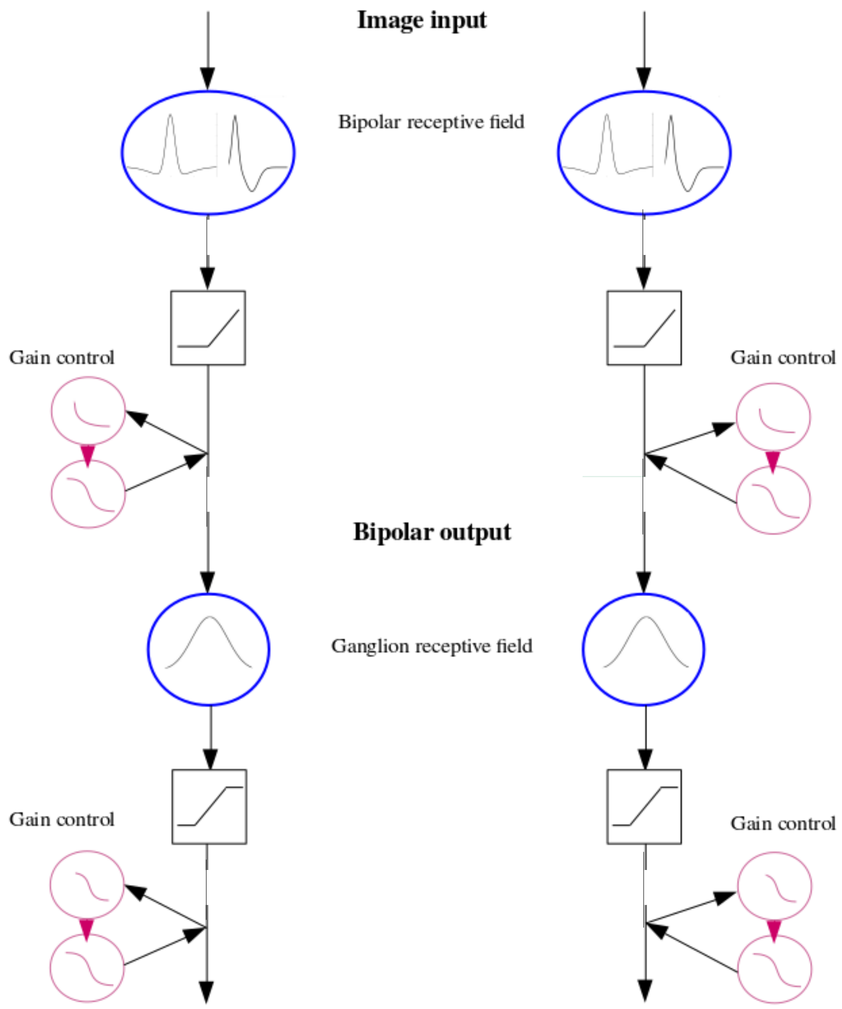
2) Gap junctions connectivity



Ganglion cells are independent encoders

Building a 2D retina model for motion anticipation

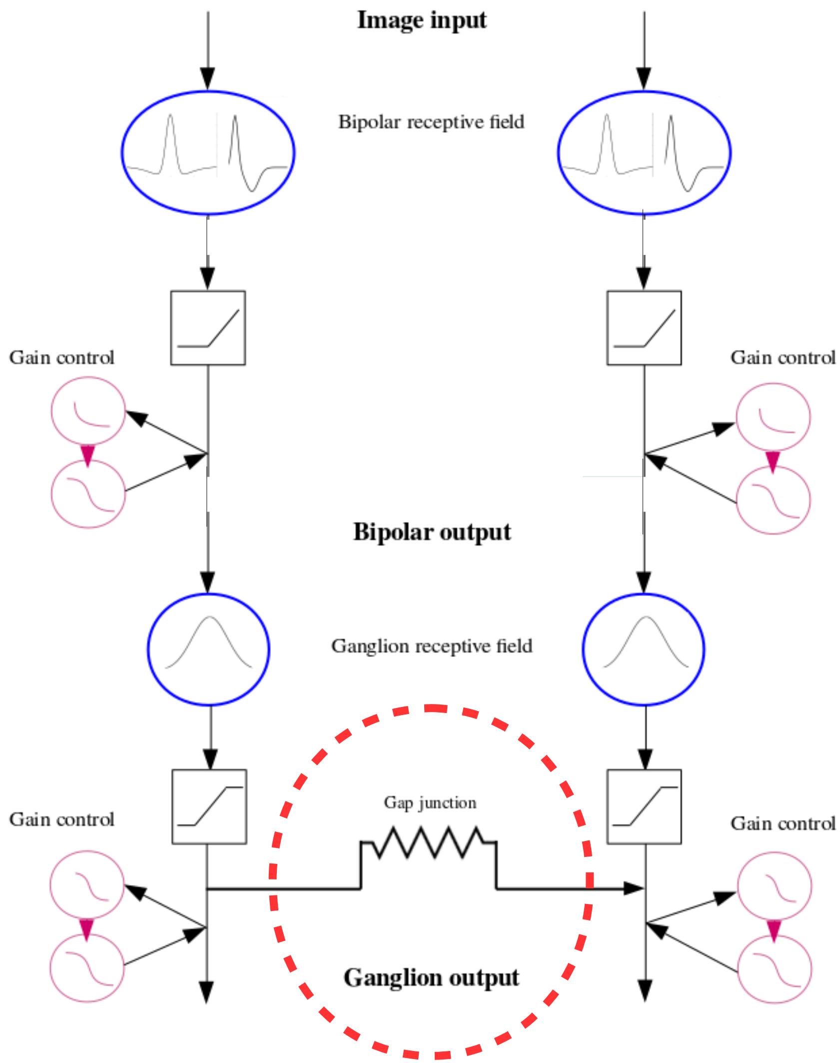
2) Gap junctions connectivity



~~Ganglion cells are independent encoders~~

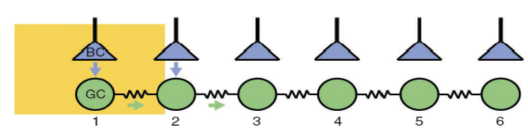
Building a 2D retina model for motion anticipation

2) Gap junctions connectivity



- A class of direction selective RGCs are connected through gap junctions

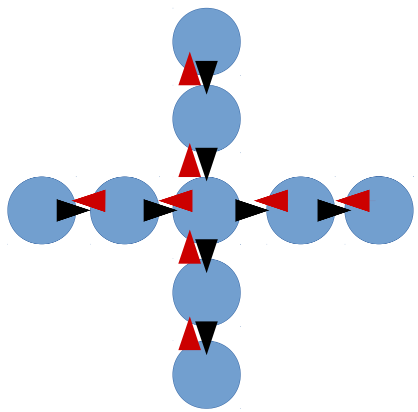
- Their activity comprises the activity pooled from bipolar cells and the activity coming from the downstream RGCs, in the direction of motion



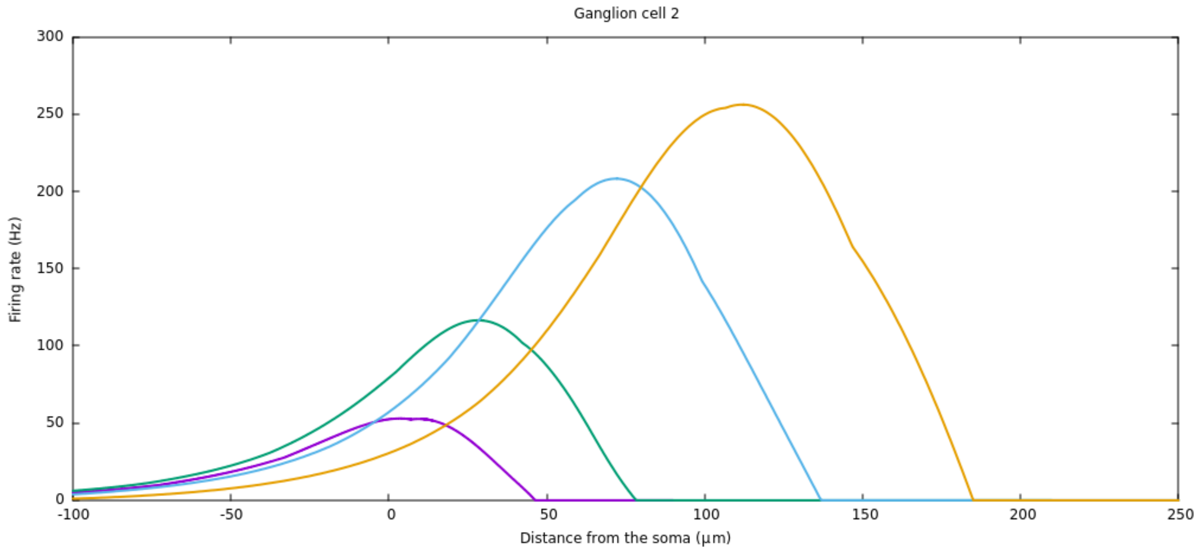
$$R_{G_{D k_D}} = V_{G_{D k_D}} + \beta \, R_{G_{D k_{D-1}}}$$

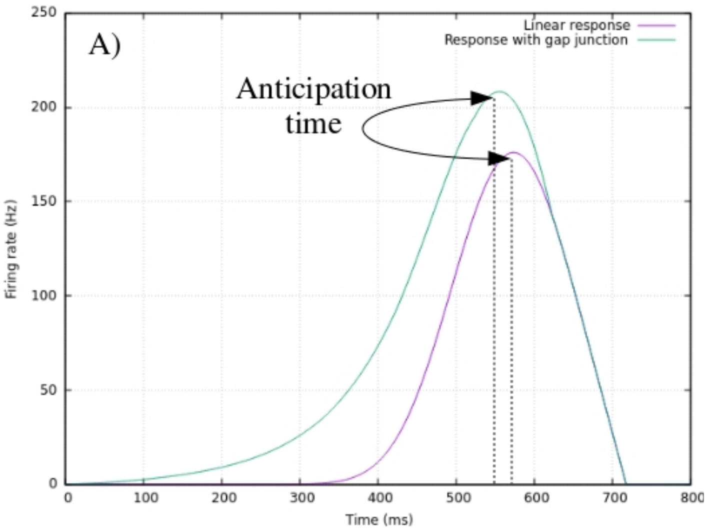
Trenholm & al. 2013

1D results : smooth motion anticipation with gap junctions



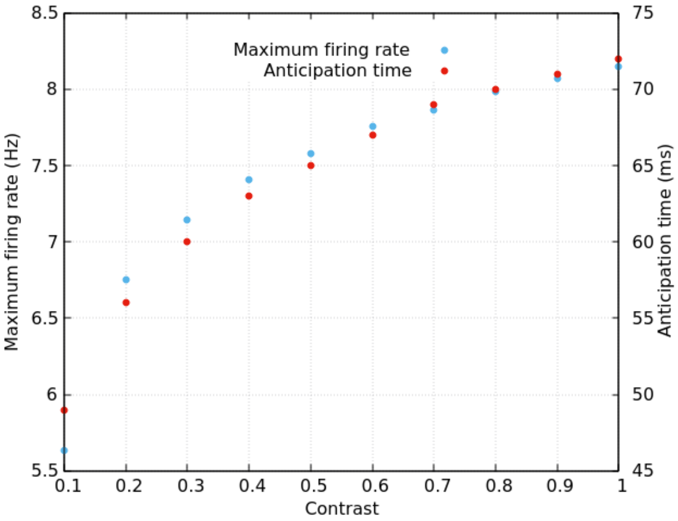
DSGCs in cardinal directions

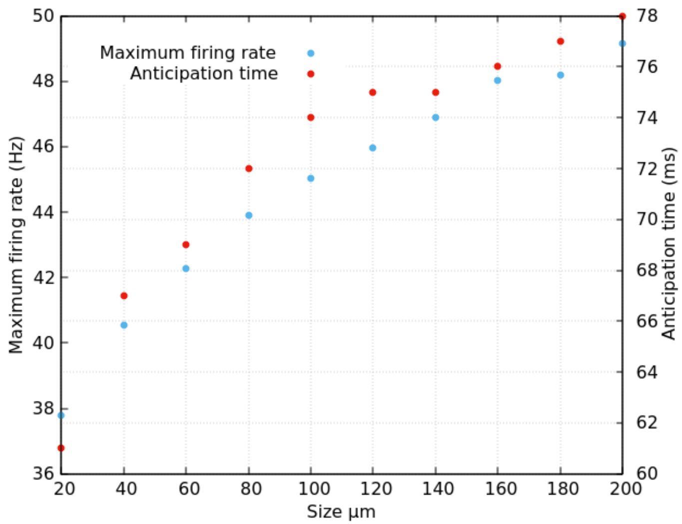


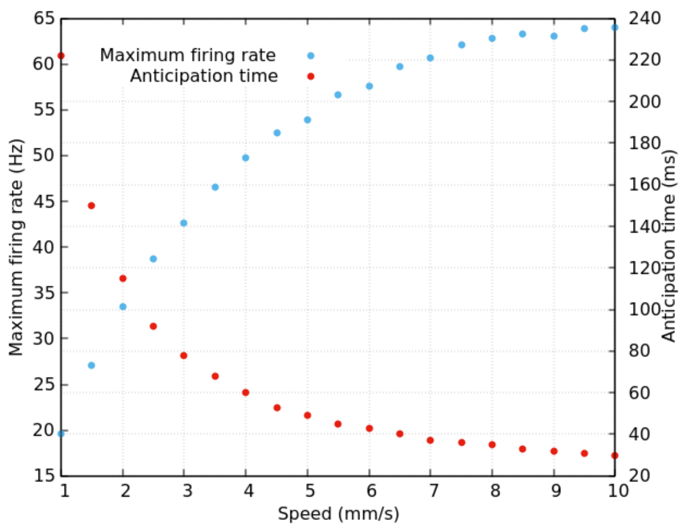


1D results : smooth motion anticipation with gap junctions

Anticipation variability with stimulus parameters



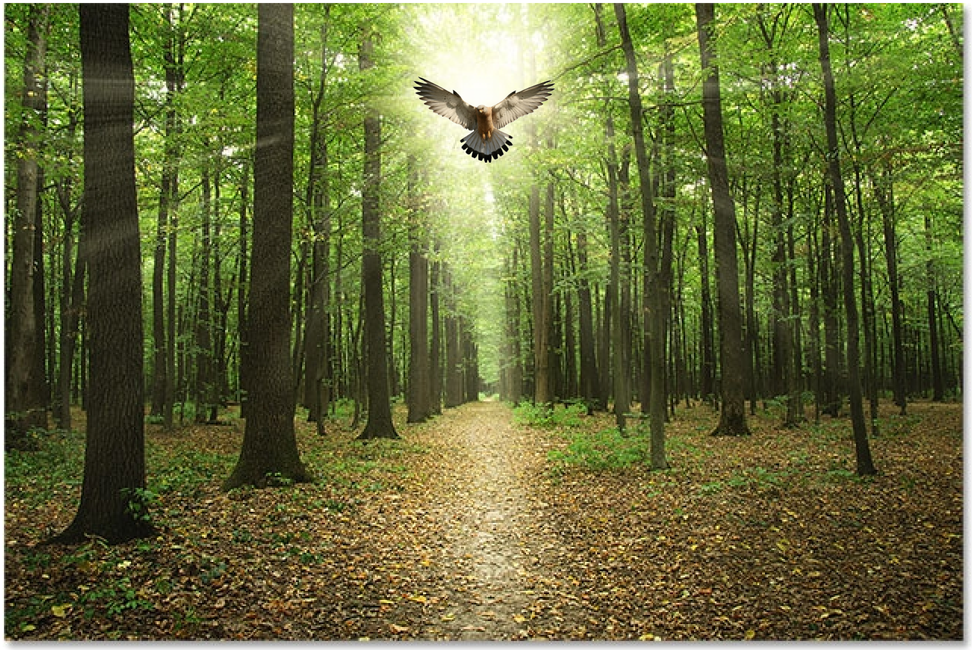




Building a 2D retina model for motion anticipation

3) Amacrine cells connectivity

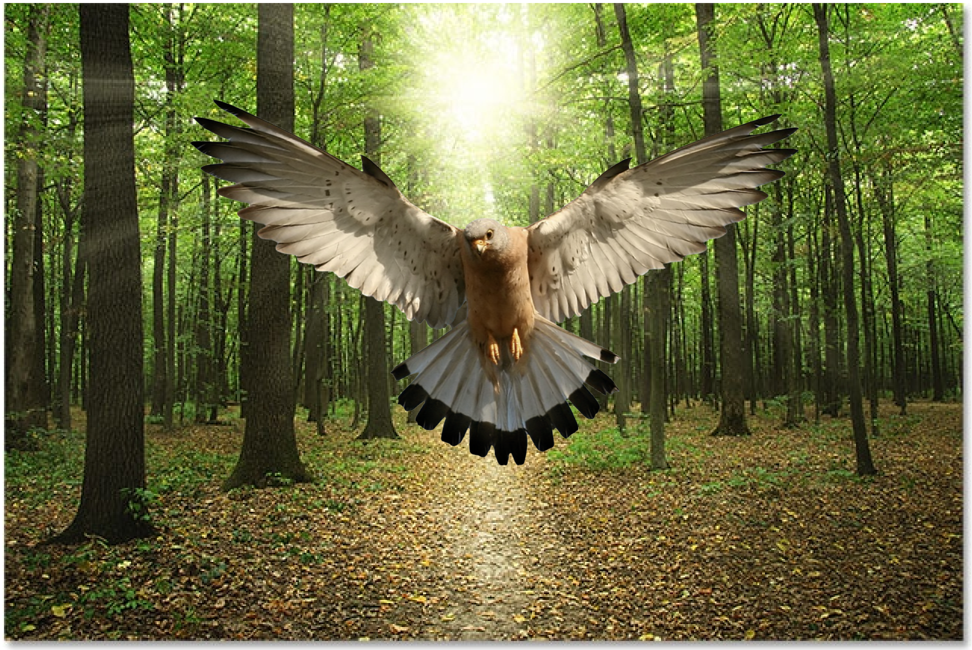
- A class of RGCs are selective to differential motion



Building a 2D retina model for motion anticipation

3) Amacrine cells connectivity

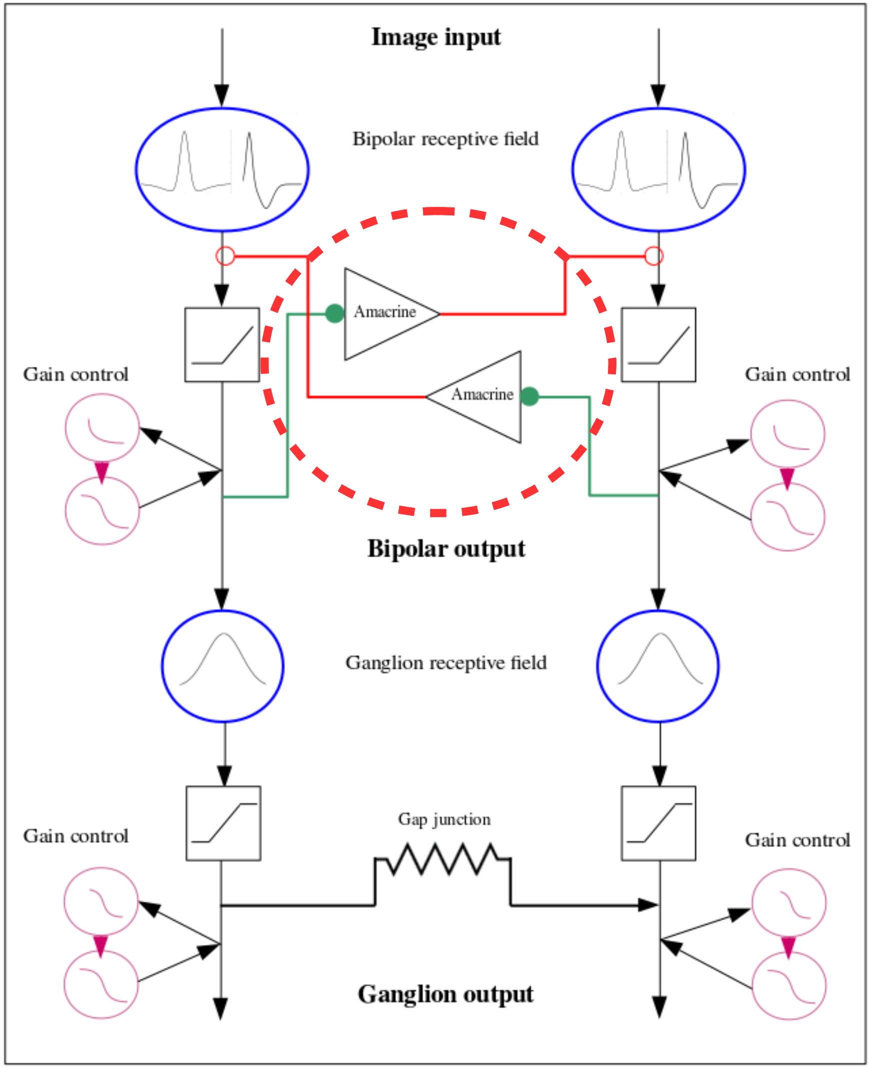
- A class of RGCs are selective to differential motion



- The circuitry involves amacrine cells connectivity upstream of ganglion cells

Connectivity pathways

2) Amacrine cells connectivity



- Bipolar voltage :

$$\frac{dV_{B_i}}{dt} = -\frac{1}{\tau_B} V_{B_i} + \sum_{j=1}^{N_A} W_{B_i}^{A_j} V_{A_j} + F_{B_i}(t).$$

- External drive :

$$F_{B_i}(t) = \left[K_i \overset{S,t}{*} \left(\frac{\mathcal{S}}{\tau_B} + \frac{d\mathcal{S}}{dt} \right) \right](t)$$

- Amacrine voltage :

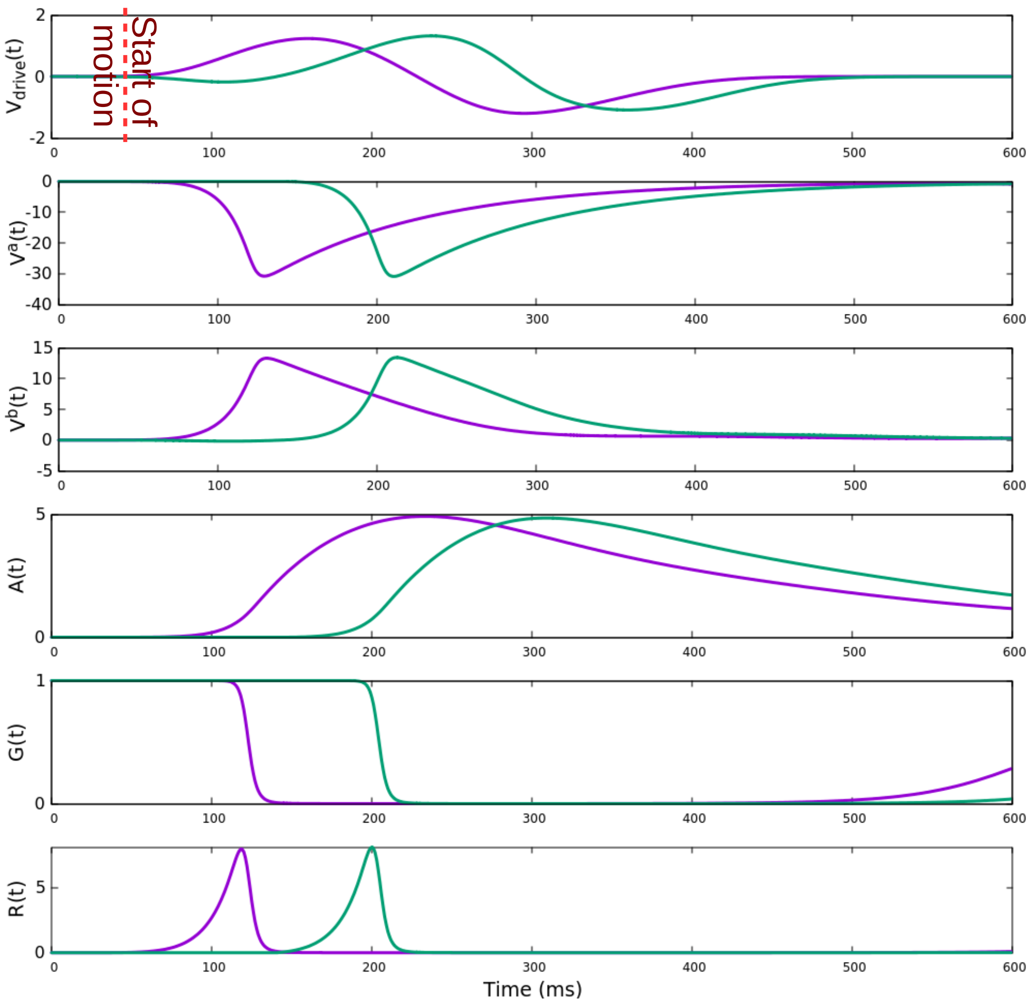
$$\frac{dV_{A_j}}{dt} = -\frac{1}{\tau_A} V_{A_j}(t) + \sum_{i=1}^{N_A} W_{A_j}^{B_i} R_{B_i}(t).$$

- Coupled dynamics :

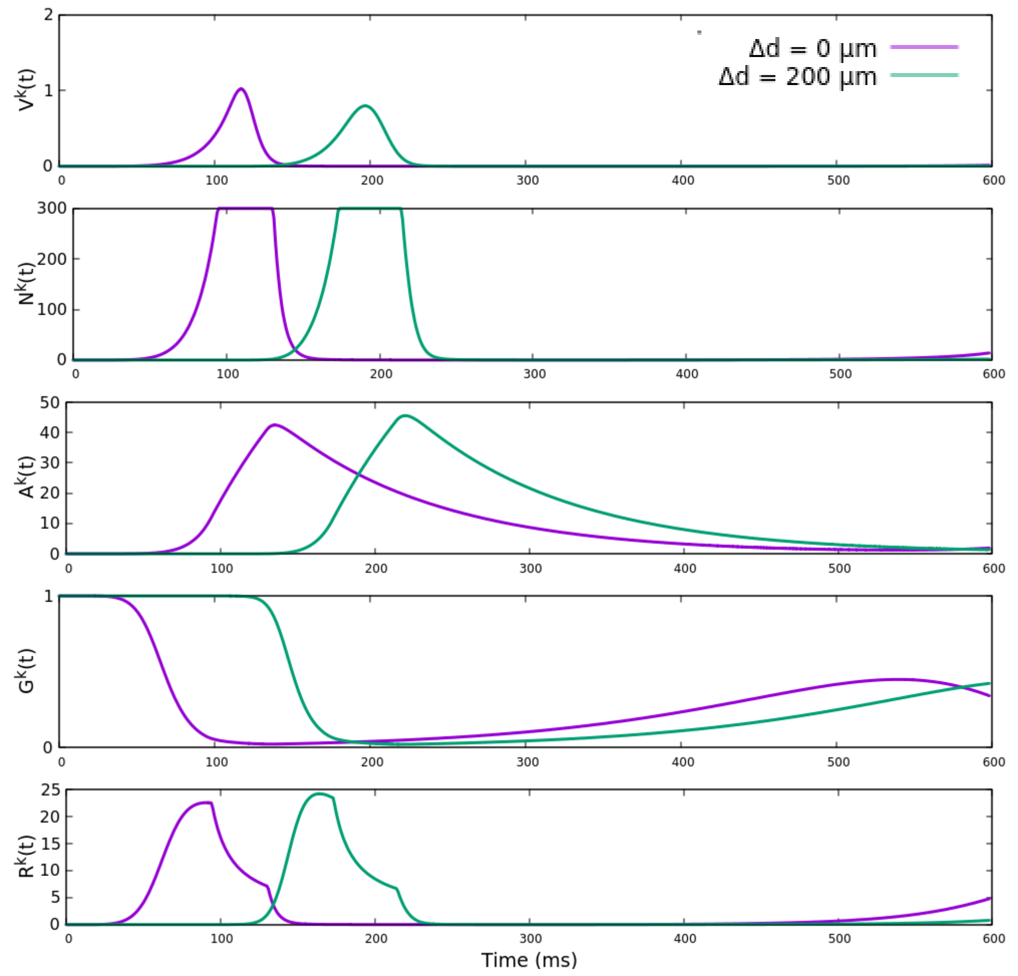
$$\begin{cases} \frac{dV_{B_i}}{dt} &= -\frac{1}{\tau_B} V_{B_i} + \sum_{j=1}^{N_A} W_{B_i}^{A_j} V_{A_j} + F_{B_i}(t) \\ \frac{dA_{B_i}}{dt} &= -\frac{A_{B_i}}{\tau_a} + h\,\mathcal{N}(V_{B_i}(t)), \\ \frac{dV_{A_j}}{dt} &= -\frac{1}{\tau_A} V_{A_j}(t) + \sum_{i=1}^{N_A} W_{A_j}^{B_i} R_{B_i}(t). \end{cases}$$

1D results : smooth motion anticipation with amacrine connectivity

Bipolar layer

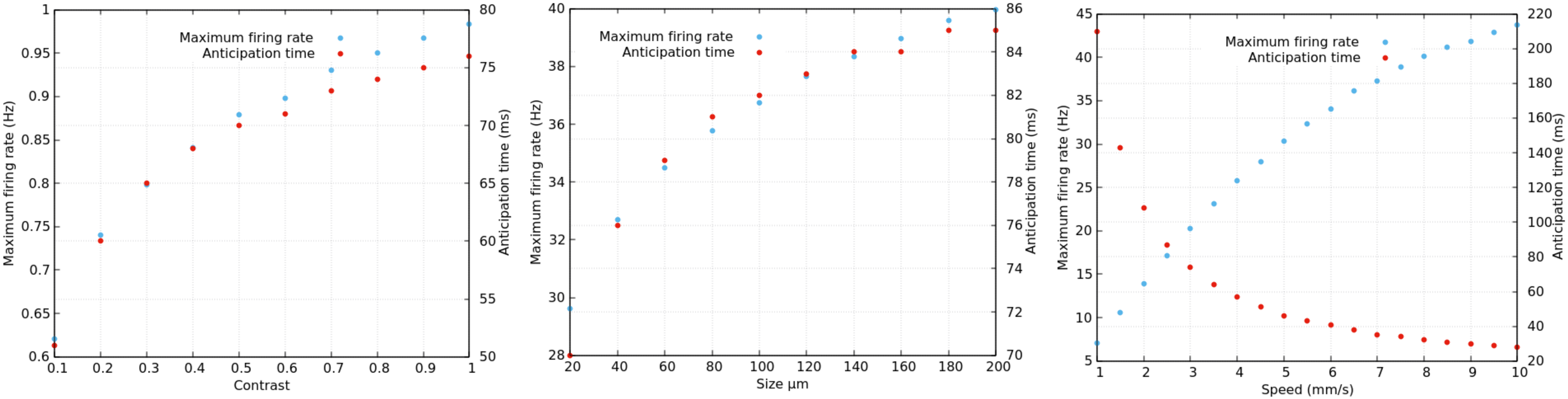


Ganglion layer

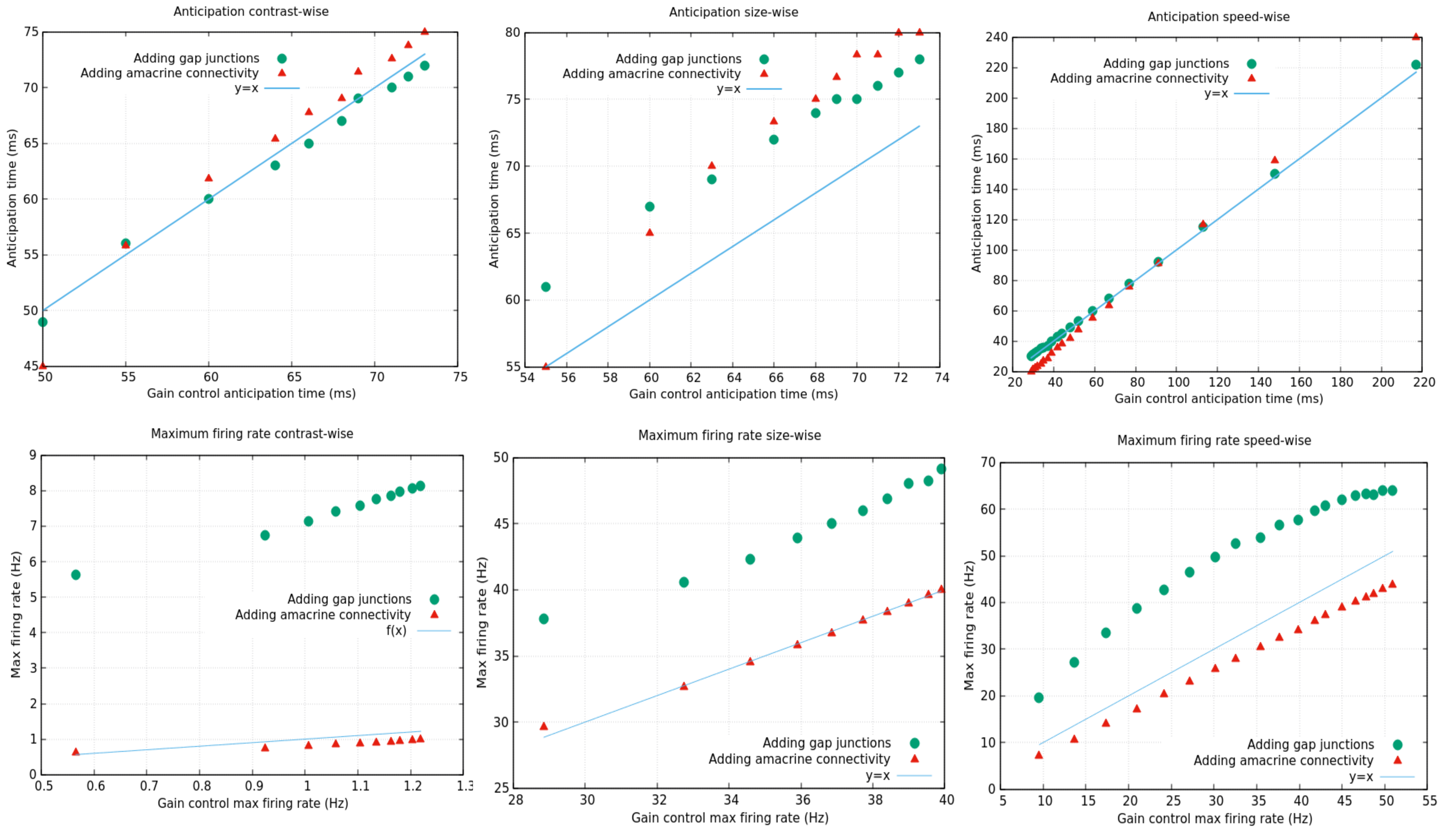


1D results : smooth motion anticipation with amacrine connectivity

Anticipation variability with stimulus parameters

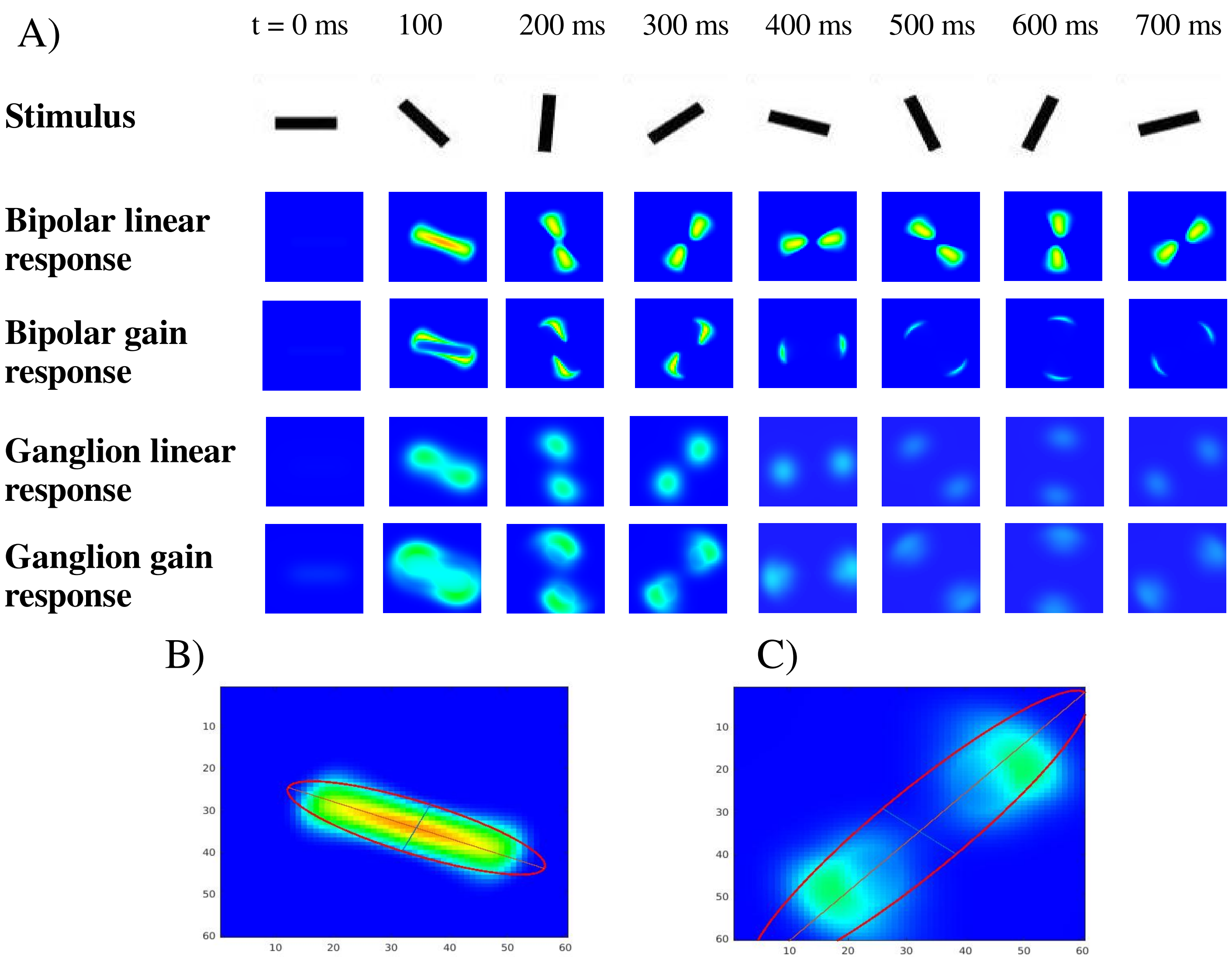


Comparing the performance of the three layers



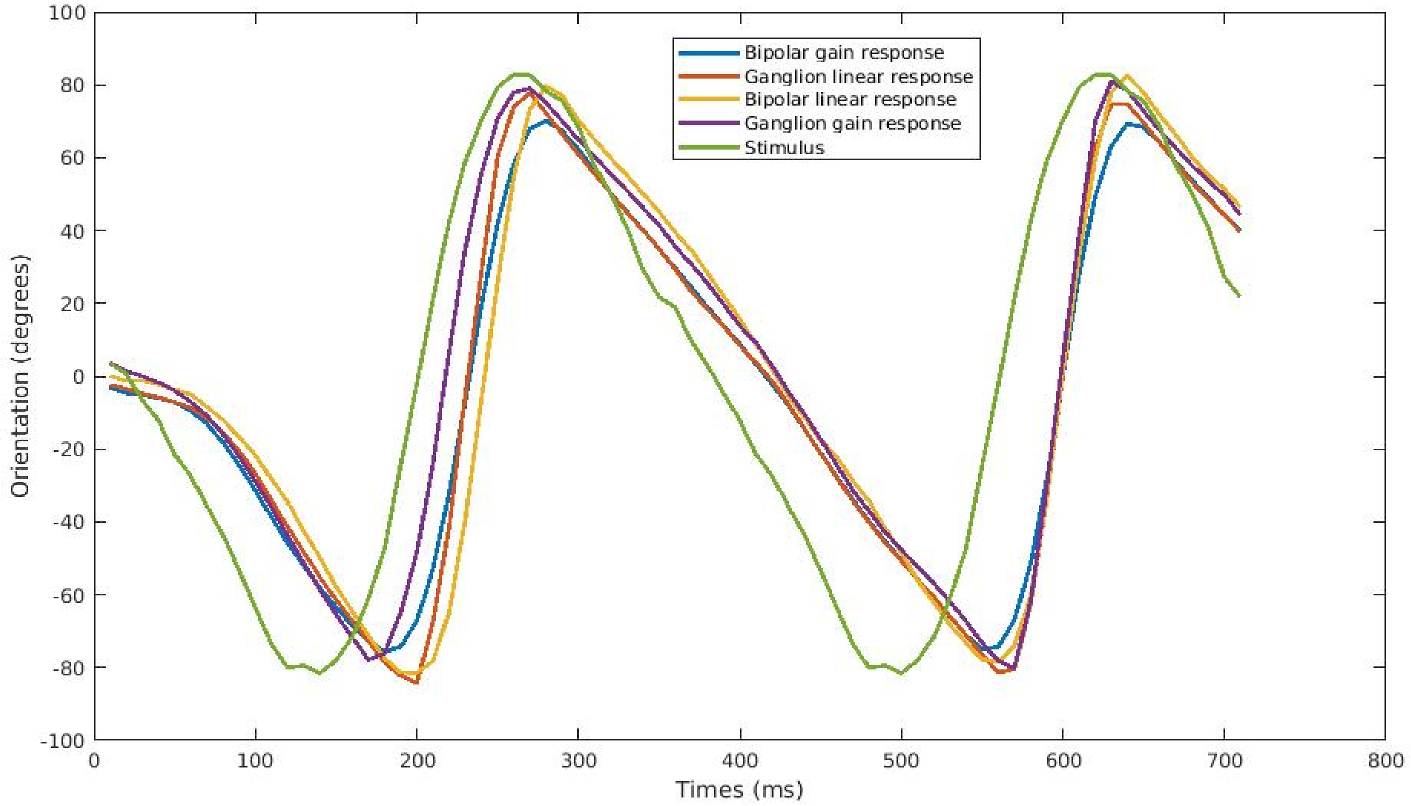
Suggesting new experiments : 2D results

1) Angular anticipation



Suggesting new experiments : 2D results

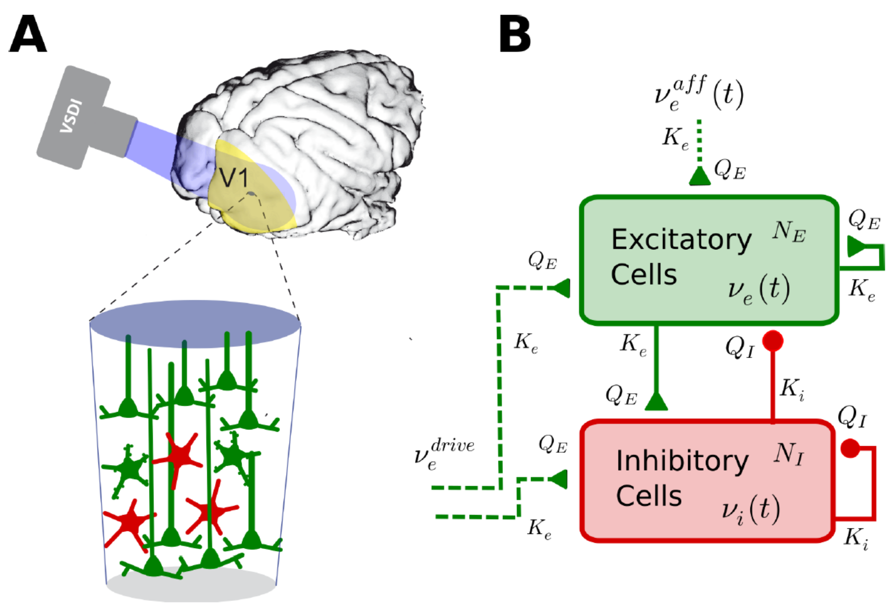
1) Angular anticipation

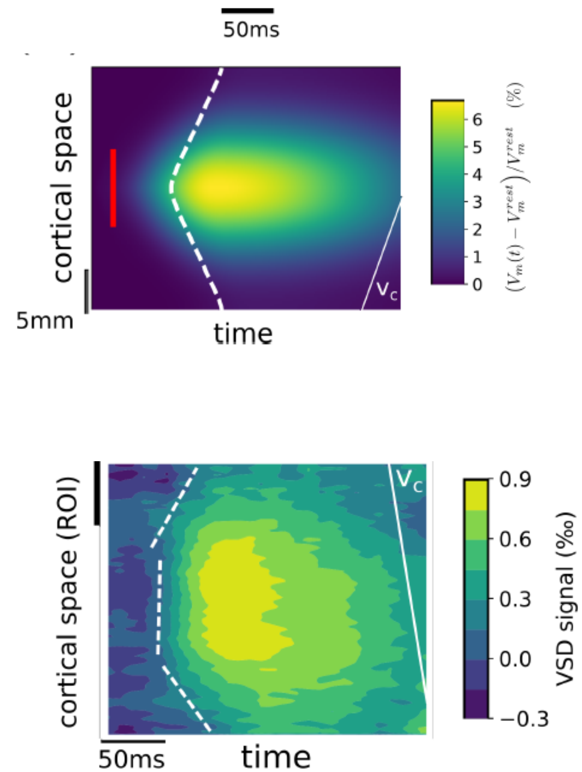


II) Anticipation in V1

A mean field model to reproduce VSDI recordings

Zerlaut et al 2016
Chemla et al 2018





A mean field model to reproduce VSDI recordings

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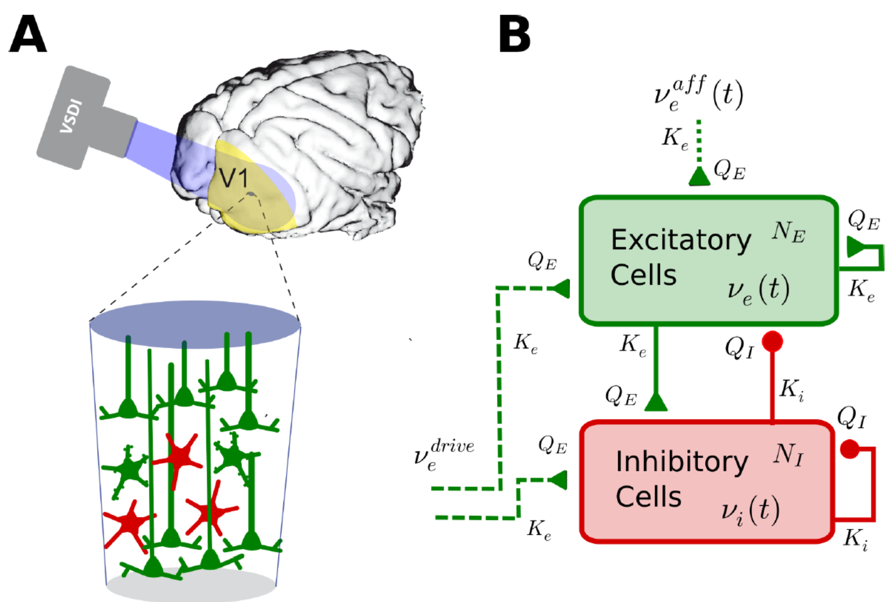
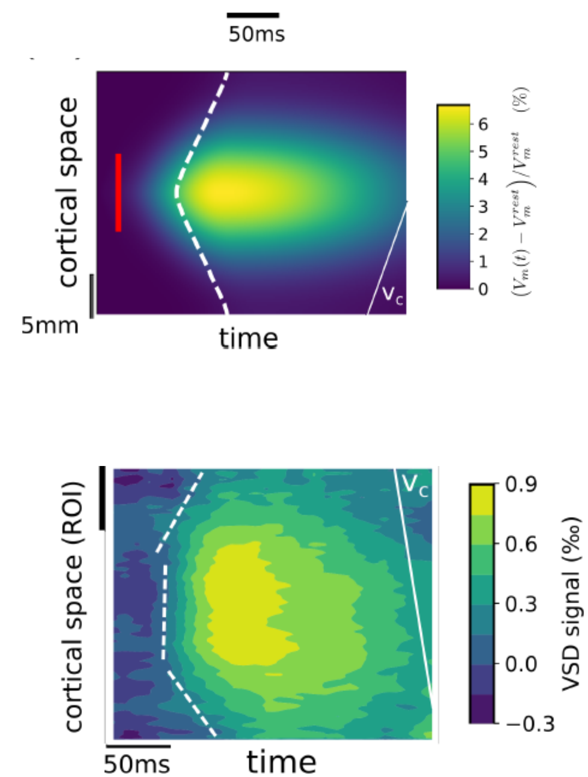




Challenge : connect our retina model to a mean field cortical model reproducing VSDI data

Cortex mean field model

Zerlaut et al 2016
Chemla et al 2018

Single neuron model → **Semi analytical transfer function** → **Mean field equations**

Single neuron model (The adaptative exponential integrate and fire model Brette and Gerstner, 2005)

$$\begin{cases} C_m \dfrac{dV}{dt} = g_L\,(E_L - V) + I_{syn}(V,t) + k_a e^{\frac{V-V_{thre}}{k_a}} - I_w \\ \tau_w \dfrac{dI_w}{dt} = -I_w + a \cdot (V - E_L) + \displaystyle\sum_{t_s \in \{t_{spike}\}} b\ \delta(t - t_s) \end{cases}$$

$$I_{syn}(V,t) = \sum_{s \in \{e,i\}} \sum_{t_s \in \{t_s\}} Q_s\,(E_s - V)\, e^{-\frac{t-t_s}{\tau_s}}\, \mathcal{H}(t - t_s)$$

Semi analytical transfer function

$$\nu_{out} = \mathcal{F}(\nu_e, \nu_i) = \frac{1}{2\,\tau_V} \cdot Erfc\left(\frac{V_{thre}^{eff} - \mu_V}{\sqrt{2}\,\sigma_V}\right)$$

$$V_{thre}^{eff}(\mu_V, \sigma_V, \tau_V^N) = P_0 + \sum_{x \in \{\mu_V, \sigma_V, \tau_V^N\}} P_x \cdot \left(\frac{x - x^0}{\delta x^0}\right) + P_{\mu_G} \log\left(\frac{\mu_G}{g_L}\right) + \sum_{x,y \in \{\mu_V, \sigma_V, \tau_V^N\}^2} P_{xy} \cdot \left(\frac{x - x^0}{\delta x^0}\right)\left(\frac{y - y^0}{\delta y^0}\right)$$

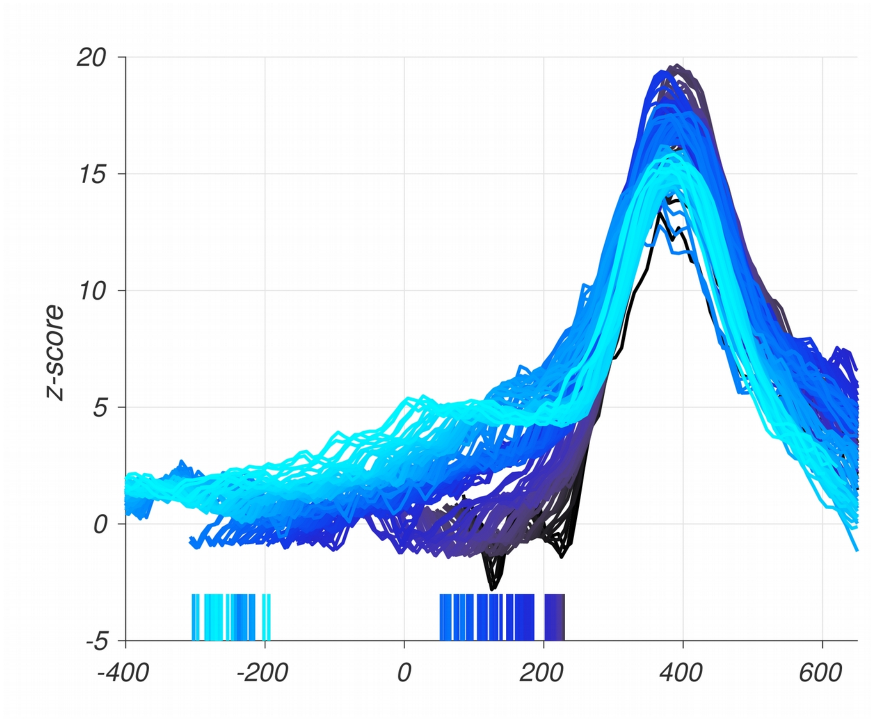
Master equation local population dynamics (El Boustani and Destexhe, 2009)

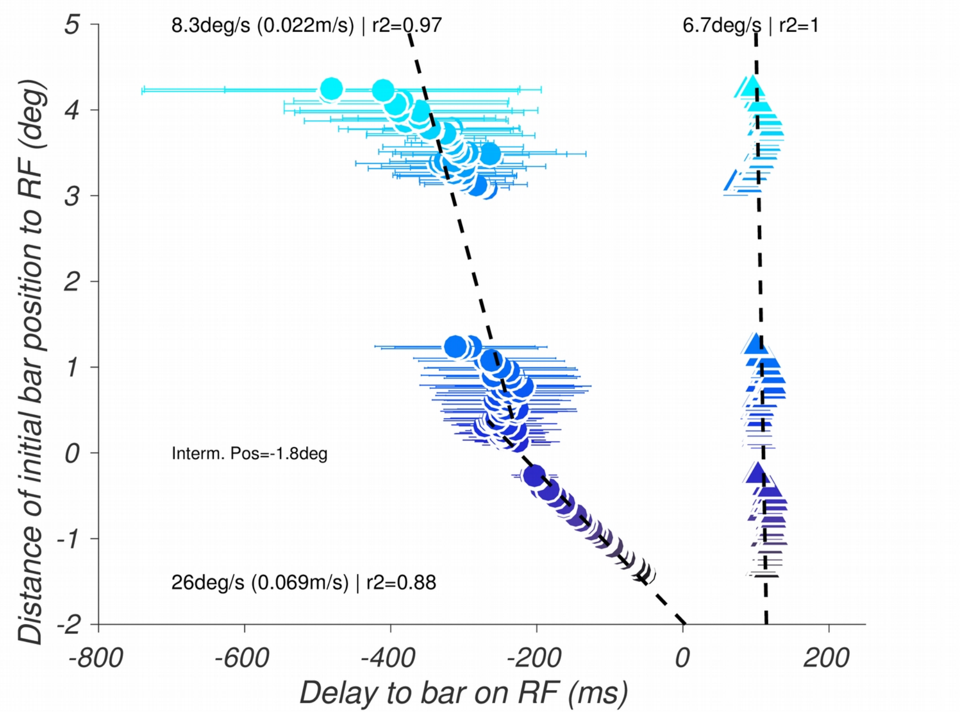
$$\begin{cases} T\,\dfrac{\partial \nu_\mu}{\partial t} = (\mathcal{F}_\mu - \nu_\mu) + \dfrac{1}{2}\, c_{\lambda\eta}\, \dfrac{\partial^2 \mathcal{F}_\mu}{\partial \nu_\lambda \partial \nu_\eta} \\ T\,\dfrac{\partial c_{\lambda\eta}}{\partial t} = A_{\lambda\eta} + (\mathcal{F}_\lambda - \nu_\lambda)\,(\mathcal{F}_\eta - \nu_\eta) + \\ \qquad c_{\lambda\mu}\, \dfrac{\partial \mathcal{F}_\mu}{\partial \nu_\lambda} + c_{\mu\eta}\, \dfrac{\partial \mathcal{F}_\mu}{\partial \nu_\eta} - 2 c_{\lambda\eta} \end{cases}$$

$$A_{\lambda\eta} = \begin{cases} \dfrac{\mathcal{F}_\lambda\,(1/T - \mathcal{F}_\lambda)}{N_\lambda} & \text{if } \lambda = \eta \\ 0 & \text{otherwise} \end{cases}$$

Anticipation in V1

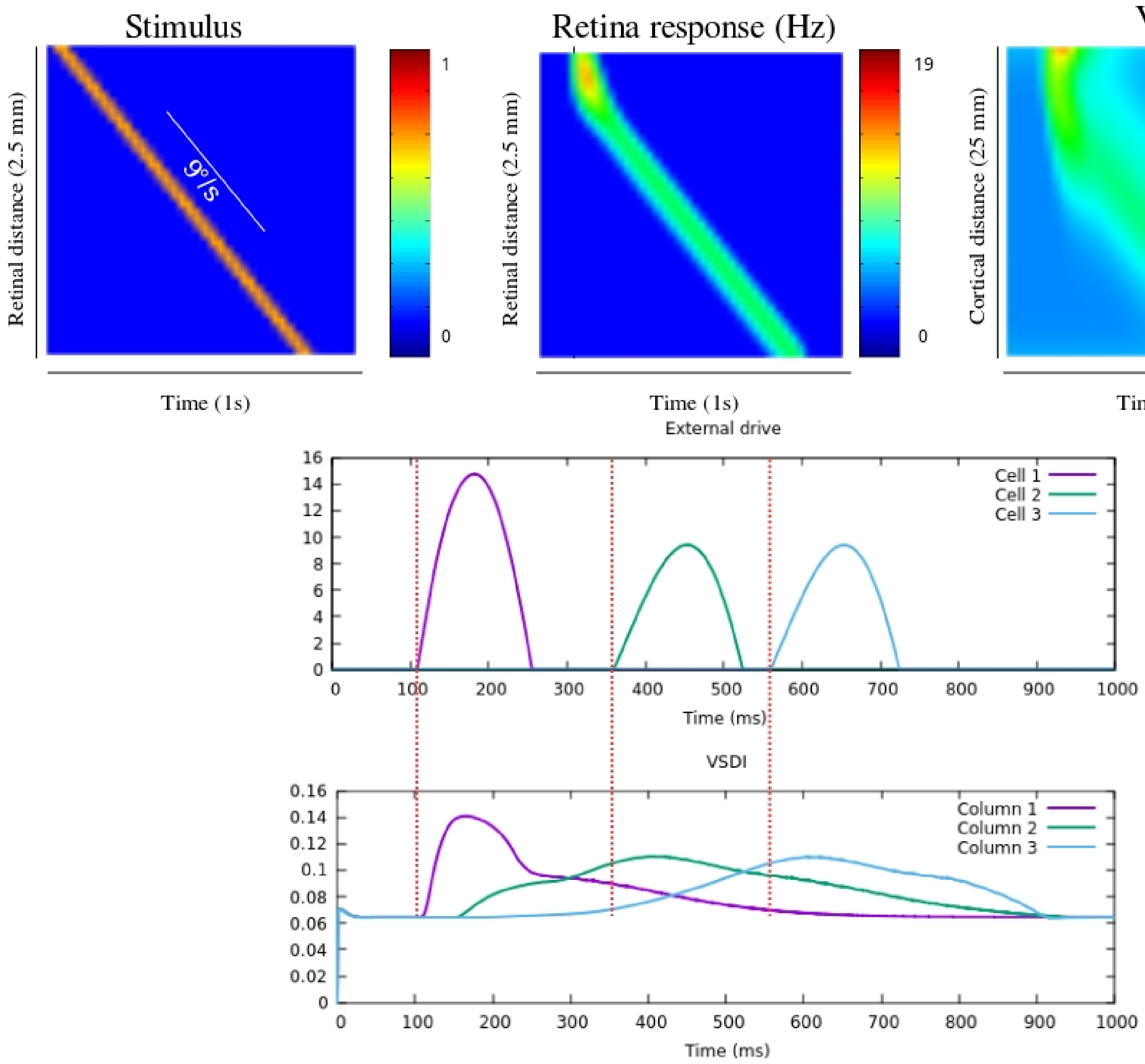
For distant bars, the activity rises earlier



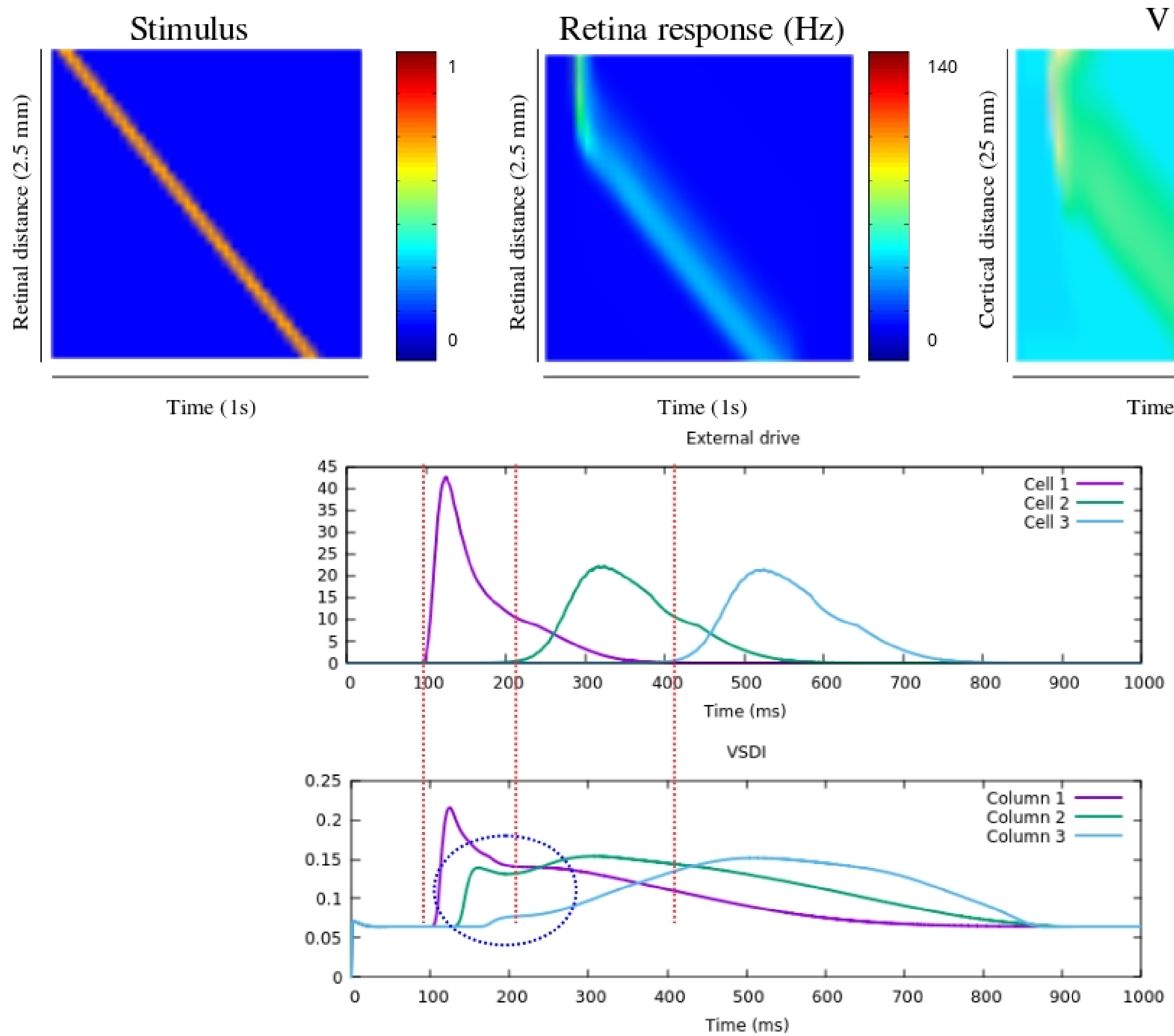


Source : Benvenutti et al. 2015

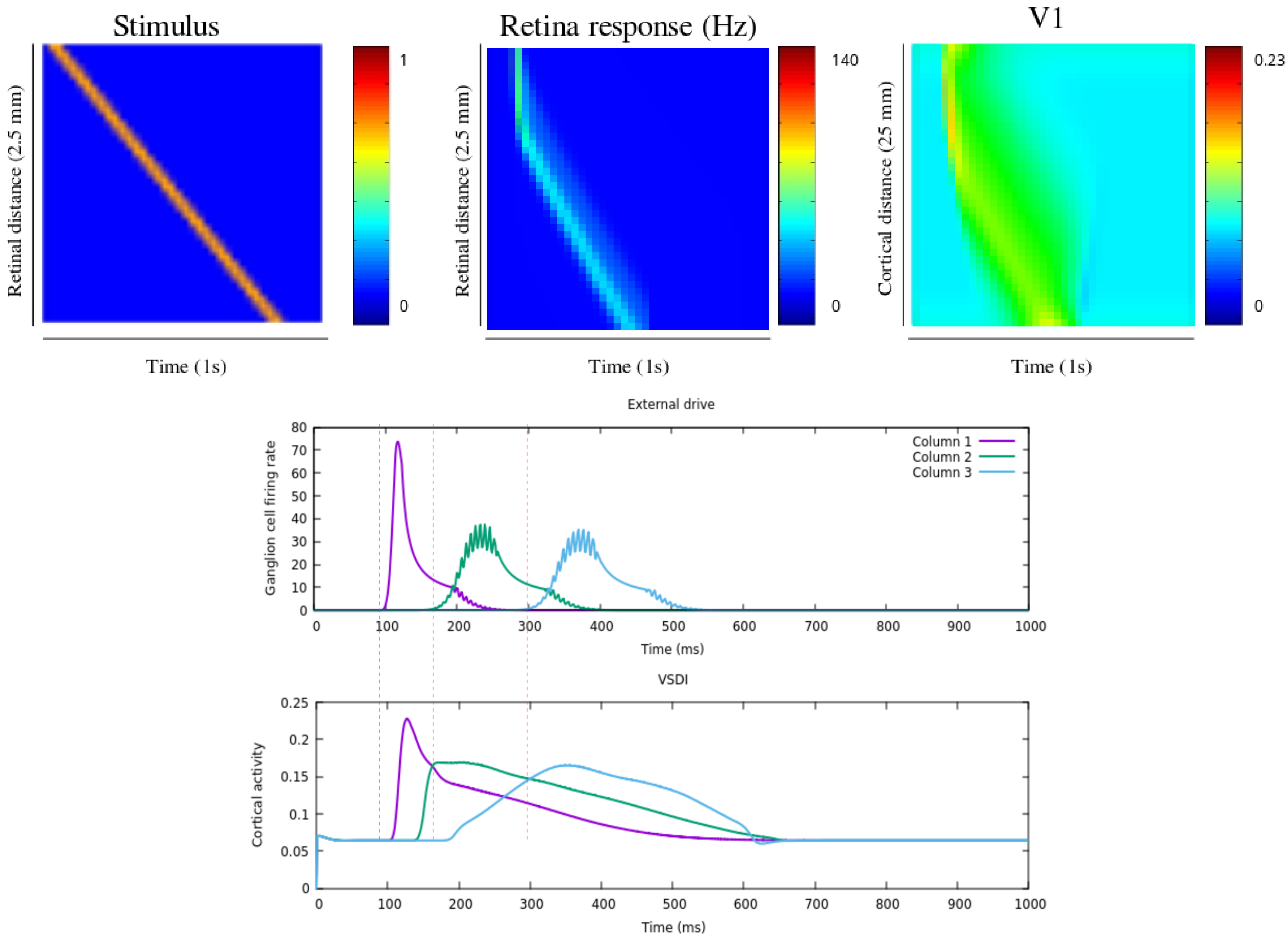
Response of the cortical model to a retina drive without gain control



Response of the cortical model to a retina drive with gain control

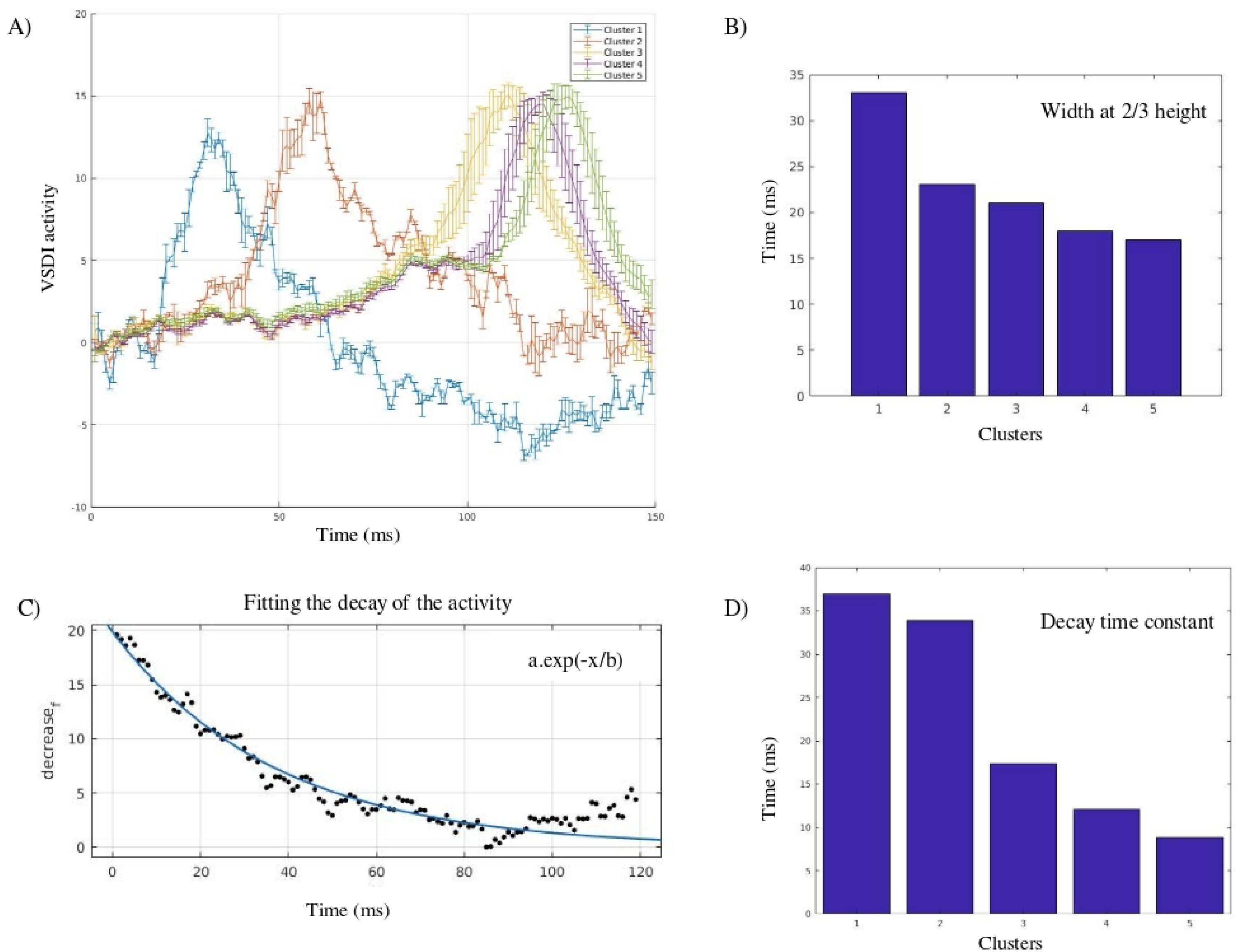


Response of the cortical model to a retina drive with amacrine connectivity

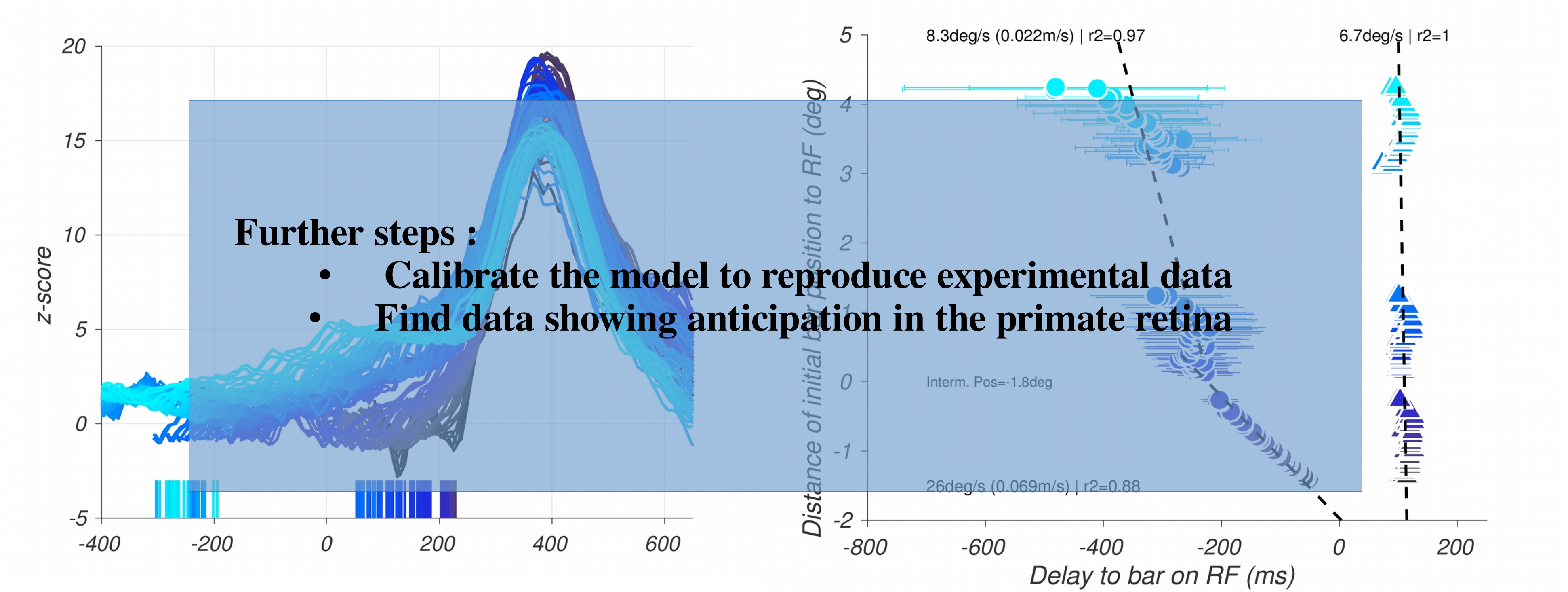


Anticipation in the cortex : VSDI data analysis

(Data courtesy of F. Chavane et S. Chemla)



Anticipation in V1



Further steps :

- **Calibrate the model to reproduce experimental data**
- **Find data showing anticipation in the primate retina**

Source : Benvenutti et al. 2015

Conclusions

Ongoing work :

- Studying analytically anticipation in the amacrine connectivity sub-model
- Studying anticipation on non-uniform backgrounds
- Assessing the effect of anticipation in the retina on the one in the cortex

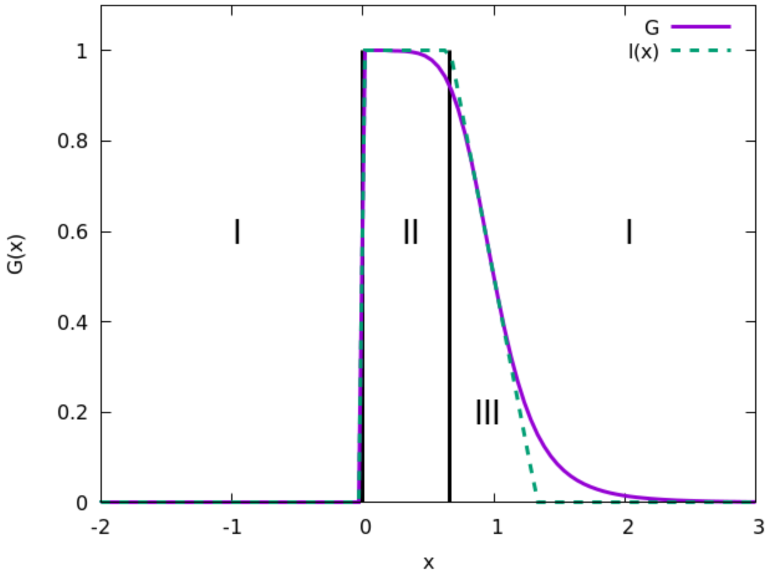
Questions :

- How to improve object identification 1) exploring the model's parameters and 2) using connectivity ?
- Is our model able to anticipate more complex trajectories, with accelerations for instance ?
- How to calibrate connectivity using biology ?
- Would it be possible to design psycho-physical tests clearly showing the role of the retina in visual anticipation ?

Thank you for your attention !

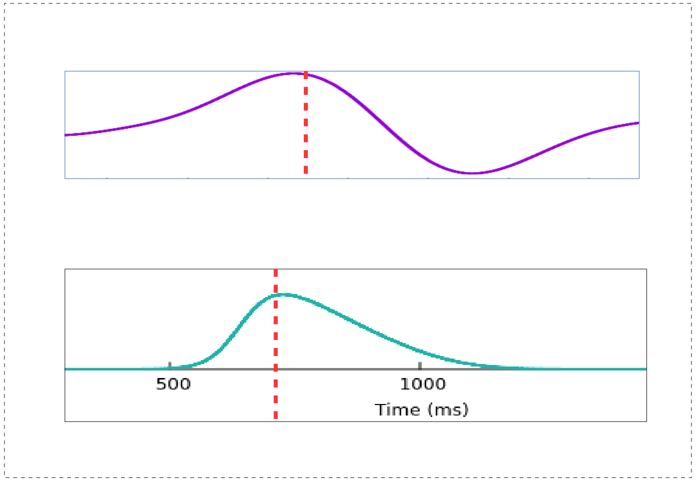
Supplementary material

How does gain control work



$$\mathcal{G}_B(A) = \begin{cases} 0, & \text{if } A \leq 0; \\ \frac{1}{1+A^6}, & \text{else.} \end{cases}$$

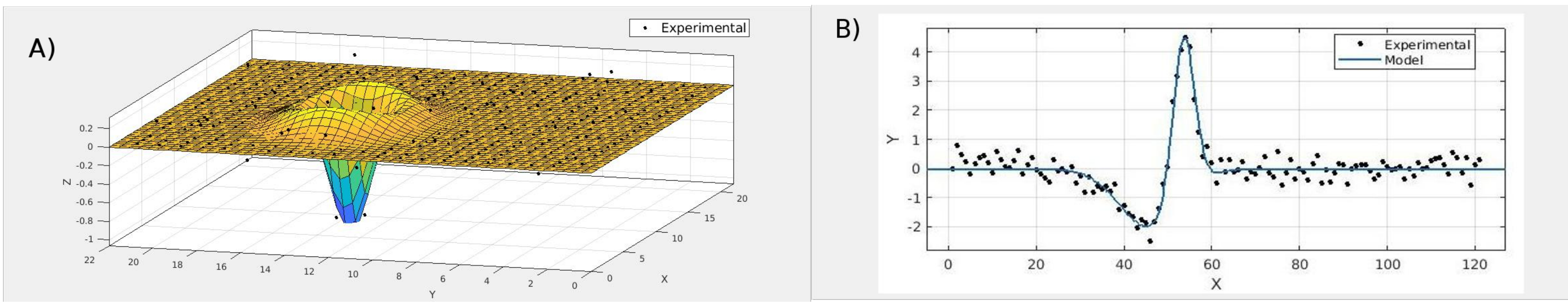
$$V_{B_i}(t)$$



$$R_{B_i} = \mathcal{N}_B\left(V_{B_i}\right)\mathcal{G}_B\left(A_{B_i}\right).$$

Stimulus integration

$$\left[K_i \overset{S,t}{*} \mathcal{S} \right](t) = \int_{-\infty}^{t} K_T(t-u) \left[\int_{\mathbb{R}^2} K_{i,S}(x,y)\, \mathcal{S}(x,y,u)\, dx\, dy \right] du \equiv V_{i_{drive}}(t).$$

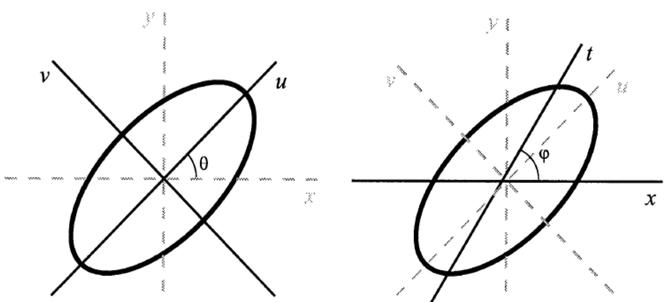


$$K_{i,S}(x,y) = \frac{A_1}{2\pi\sqrt{\det C_1}}\, e^{-\frac{1}{2}\tilde{X}_i.C_1^{-1}.X_i} - \frac{A_2}{2\pi\sqrt{\det C_2}}\, e^{-\frac{1}{2}\tilde{X}_i.C_2^{-1}.X_i},$$

$$K_T(t) = \left(\frac{K_1}{\sqrt{2\pi}\sigma_1}\, e^{-\frac{(t-\mu_1)^2}{2\sigma_1^2}} - \frac{K_2}{\sqrt{2\pi}\sigma_2}\, e^{-\frac{(t-\mu_2)^2}{2\sigma_2^2}} \right) H(t)$$

(Data courtesy of O. Marre)

Stimulus integration : anisotropy



Geusebroek et al. 2003

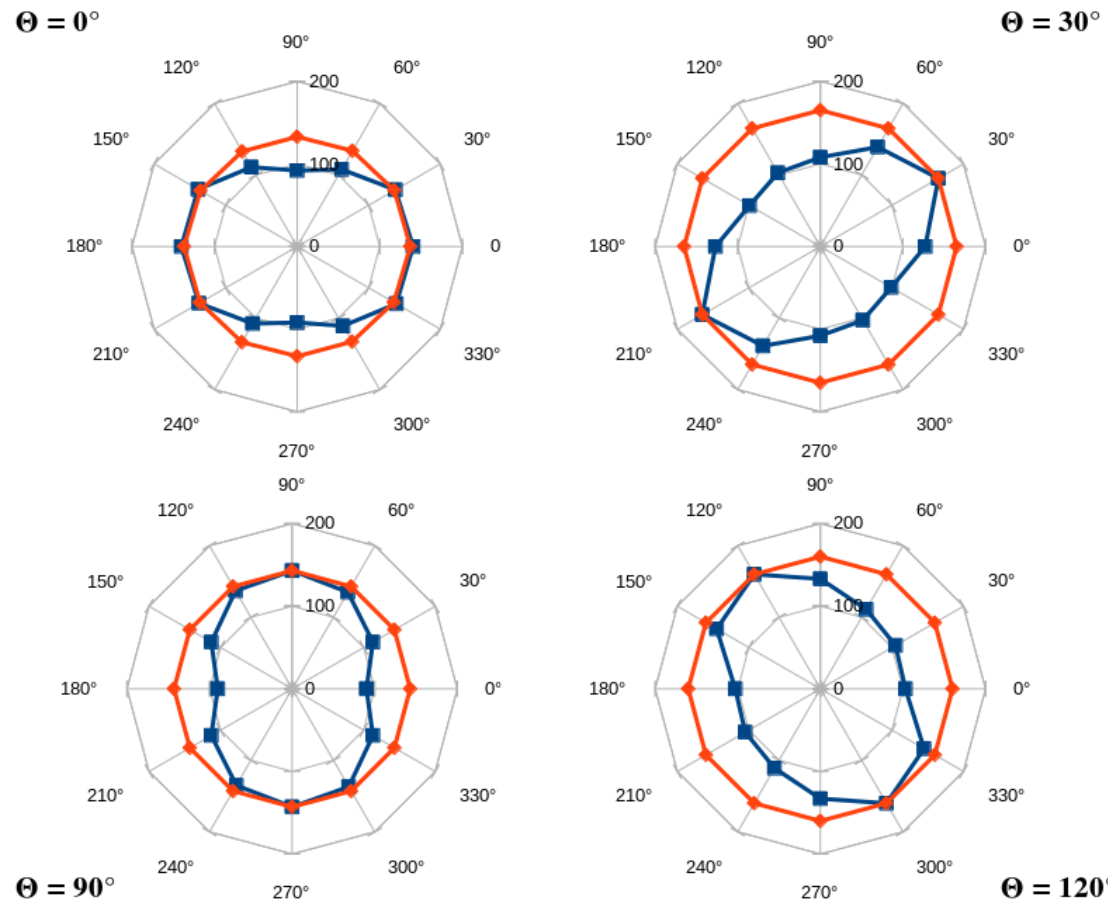
$$\sigma_{x'} = \frac{\sigma_x \sigma_y}{\sqrt{\sigma_x^2 \cos\theta^2 + \sigma_y^2 \sin\theta^2}}$$

$$\sigma_\phi = \frac{\sqrt{\sigma_y^2 \cos\theta^2 + \sigma_x^2 \sin\theta^2}}{\sin\phi}$$

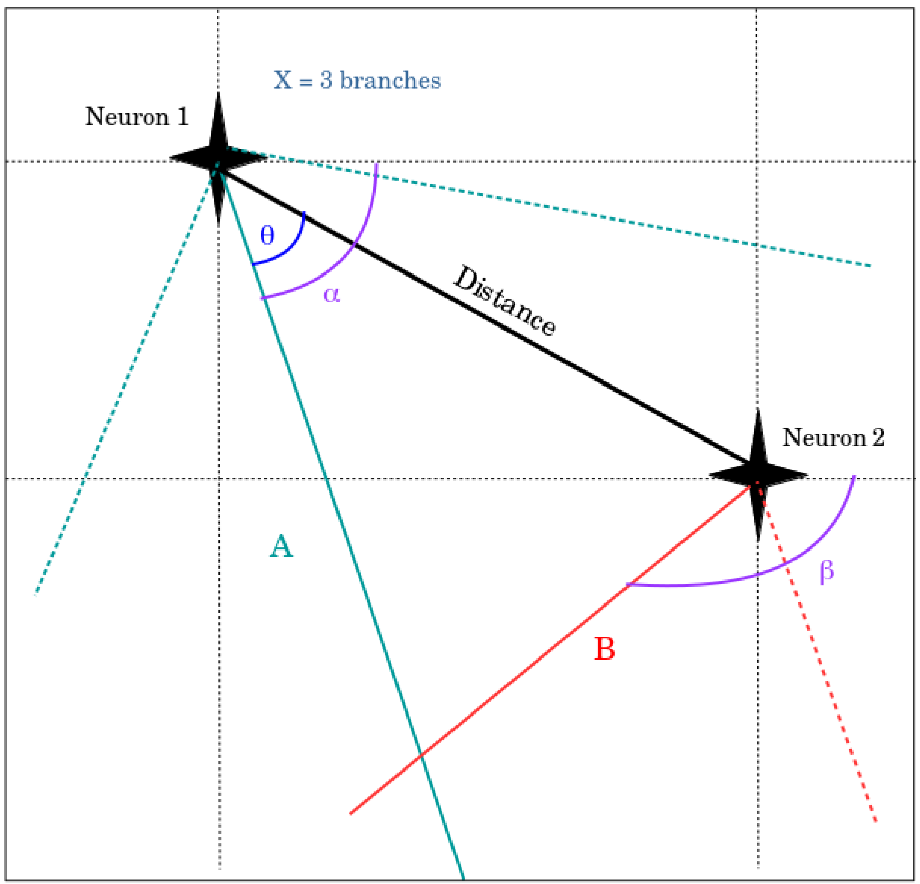
$$\tan(\phi) = \frac{\sigma_y^2 \cos\theta^2 + \sigma_x^2 \sin\theta^2}{(\sigma^2 - \sigma_y^2)\cos\theta \sin\theta}$$

$$I = \sigma_{x'} \sqrt{\frac{\pi}{2}} \sum_{(i;j)\in[0,s_x]\times[0,s_y]} \int_{y\frac{\delta}{\sin(\phi)}}^{(y+1)\frac{\delta}{\sin(\phi)}} C_{ij} e^{\frac{(y'-y_0')^2}{2\sigma_\phi^2}}$$

$$[erf(\frac{(-\cos(\phi)y' + x + 1)\delta - x_0'}{\sqrt{2}\sigma_{x'}}) - erf(\frac{(-\cos(\phi)y' + x)\delta - x_0'}{\sqrt{2}\sigma_{x'}})]dy'$$



Connectivity graph



- Variables of the model :
- Number of branches N
- Branch length X
- Branch angle α

$$F_X(x) = \int_0^1 \frac{1}{\pi\sqrt{1-\delta^2}} \frac{\mathrm{x}}{\mathrm{x}+\delta} \mathrm{d}\delta$$

$$\sin\left(\beta + \frac{\arcsin|y_j - y_i|}{\sqrt{(x_j - y_i)^2 + (y_j - x_j)^2}}\right)$$

Cortex mean field model

Zerlaut et al 2016
Chemla et al 2018

Single neuron model (The adaptative exponential integrate and fire model Brette and Gerstner, 2005)

$$\begin{cases} C_m \dfrac{dV}{dt} = g_L\,(E_L - V) + I_{syn}(V,t) + k_a e^{\frac{V - V_{thre}}{k_a}} - I_w \\ \tau_w \dfrac{dI_w}{dt} = -I_w + a \cdot (V - E_L) + \displaystyle\sum_{t_s \in \{t_{spike}\}} b\ \delta(t - t_s) \end{cases}$$

The conductance-based exponential synapse

$$I_{syn}(V,t) = \sum_{s \in \{e,i\}} \sum_{t_s \in \{t_s\}} Q_s\,(E_s - V)\, e^{-\frac{t - t_s}{\tau_s}}\, \mathcal{H}(t - t_s)$$

Semi analytical transfer function :

$$\nu_{out} = \mathcal{F}(\nu_e, \nu_i) = \frac{1}{2\,\tau_V} \cdot Erfc\Big(\frac{V_{thre}^{eff} - \mu_V}{\sqrt{2}\,\sigma_V}\Big) \quad \text{with} \quad V_{thre}^{eff}(\mu_V, \sigma_V, \tau_V^N) = P_0 + \sum_{x \in \{\mu_V, \sigma_V, \tau_V^N\}} P_x \cdot \Big(\frac{x - x^0}{\delta x^0}\Big) + P_{\mu_G} \log\Big(\frac{\mu_G}{g_L}\Big)$$

$$+ \sum_{x,y \in \{\mu_V, \sigma_V, \tau_V^N\}^2} P_{xy} \cdot \Big(\frac{x - x^0}{\delta x^0}\Big) \Big(\frac{y - y^0}{\delta y^0}\Big)$$

Cortex mean field model

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Chemla et al 2018

The mean, standard deviation and auto-correlation time of the excitatory and inhibitory conductance read :

$$\mu_{Ge}(\nu_e,\nu_i) = \nu_e\, K_e\, \tau_e\, Q_e$$

$$\sigma_{Ge}(\nu_e,\nu_i) = \sqrt{\frac{\nu_e\, K_e\, \tau_e}{2}}\, Q_e$$

$$\mu_{Gi}(\nu_e,\nu_i) = \nu_i\, K_i\, \tau_i\, Q_i$$

$$\sigma_{Gi}(\nu_e,\nu_i) = \sqrt{\frac{\nu_i\, K_i\, \tau_i}{2}}\, Q_i$$

$$\mu_G(\nu_e,\nu_i) = \mu_{Ge} + \mu_{Gi} + g_L$$

$$\tau_m(\nu_e,\nu_i) = \frac{C_m}{\mu_G}$$

$$\mu_V(\nu_e,\nu_i) = \frac{\mu_{Ge}\, E_e + \mu_{Gi}\, E_i + g_L\, E_L}{\mu_G}$$

$$\sigma_V(\nu_e,\nu_i) = \sqrt{\sum_s K_s\, \nu_s\, \frac{(U_s\cdot\tau_s)^2}{2\,(\tau_m^{\mathrm{eff}} + \tau_s)}}$$

$$\tau_V(\nu_e,\nu_i) = \Big(\frac{\sum_s \big(K_s\, \nu_s\, (U_s\cdot\tau_s)^2\big)}{\sum_s \big(K_s\, \nu_s\, (U_s\cdot\tau_s)^2/(\tau_m^{\mathrm{eff}} + \tau_s)\big)}\Big)$$

Finally, the transfer function reads :

$$\nu_{out} = \mathcal{F}(\nu_e,\nu_i) = \frac{1}{2\,\tau_V}\cdot Erfc\Big(\frac{V_{thre}^{eff} - \mu_V}{\sqrt{2}\,\sigma_V}\Big)$$

Cortex mean field model

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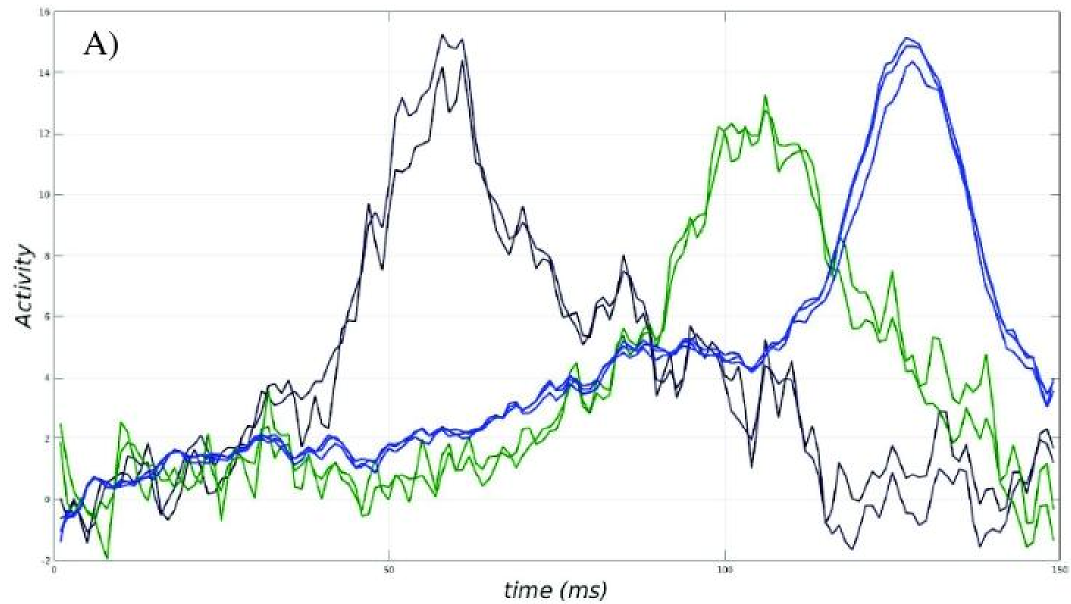
Master equation for first and second moments local population dynamics (El Boustani and Destexhe, 2009) read :

$$\begin{cases} T\,\dfrac{\partial \nu_\mu}{\partial t} = (\mathcal{F}_\mu - \nu_\mu) + \dfrac{1}{2}\, c_{\lambda\eta}\, \dfrac{\partial^2 \mathcal{F}_\mu}{\partial \nu_\lambda \partial \nu_\eta} \\ T\,\dfrac{\partial c_{\lambda\eta}}{\partial t} = A_{\lambda\eta} + (\mathcal{F}_\lambda - \nu_\lambda)\,(\mathcal{F}_\eta - \nu_\eta) + \\ \qquad c_{\lambda\mu}\dfrac{\partial \mathcal{F}_\mu}{\partial \nu_\lambda} + c_{\mu\eta}\dfrac{\partial \mathcal{F}_\mu}{\partial \nu_\eta} - 2c_{\lambda\eta} \end{cases} \longrightarrow \quad T\,\dfrac{\partial \nu_\mu}{\partial t} = \mathcal{F}_\mu - \nu_\mu$$

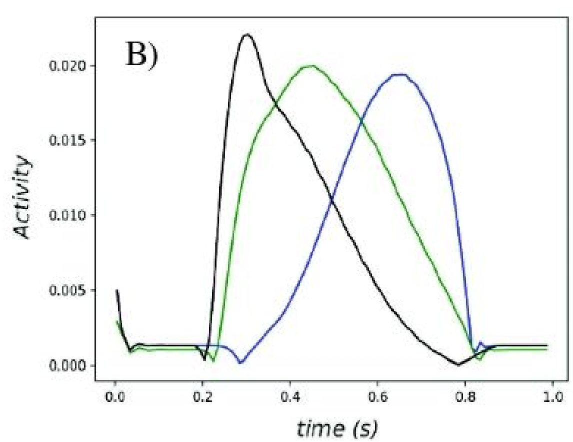
$$A_{\lambda\eta} = \begin{cases} \dfrac{\mathcal{F}_\lambda\,(1/T - \mathcal{F}_\lambda)}{N_\lambda} & \text{if } \lambda = \eta \\ 0 & \text{otherwise} \end{cases}$$

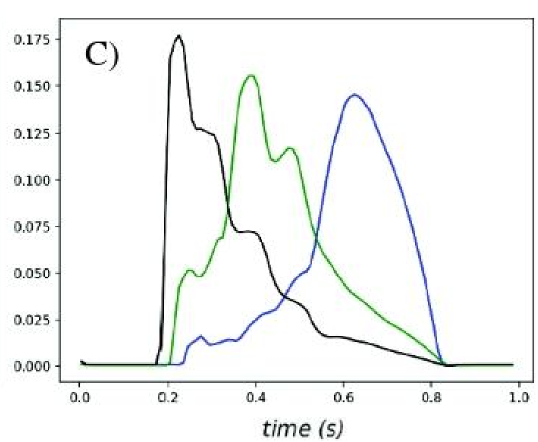
Comparing simulation results to VSDI recordings

Cortex experimental recordings



Simulation results
Response to an LN model of the retina





Simulation results
Response to a gain control model of the retina